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PALEONTOLOGY

Volume 25 NOVEMBER, 1951 Number 6

JOURNAL OF PALEONTOLOGY

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PALEOBOTANY OF THE DEVONIAN-MISSISSIPPIAN BLACK SHALES[1]

A. T. CROSS AND J. H. HOSKINS

West Virginia Geological Survey and University and University of Cincinnati

ABSTRACT—The floral assemblages of the Devonian-Mississippian black shales from the east-central interior of the United States are reviewed and contrasted with the typical Devonian and the pre-Pennsylvanian type of later Mississippian floras of North America. The flora of the New Albany-Ohio black shale complex is divisible into two groups, the Upper Devonian *Callixylon Newberryi-Foerstia-"Sporangites"* type, and the Lower Mississippian flora of more than 25 genera based on petrified wood fragments. The similarity of this unique upper New Albany flora to those found in comparable horizons of France, Scotland, Saxony and Thuringia is noted. Some conclusions based on the geographic distribution of these fossils and on the nature of the fossils themselves are discussed briefly.

INTRODUCTION

BLACK shales of Devonian and Mississippian age are widely distributed in North America. They are particularly common in eastern and central United States where they are found generally rising in the stratigraphic sequence from the Middle Devonian in New York, with some interruptions, to the Lower Mississippian (Kinderhookian) in the east-central interior both east and west of the Cincinnati Arch (fig. 2). They are also found in Montana, Idaho, New Mexico, Alberta and Alaska, but these outlying areas are not of principal interest here because of the paucity of the floras recorded from them.

[1] This paper, part of the Symposium on Applied Paleobotany, was read by A. T. Cross before the Society of Economic Paleotologists and Mineralogists at its 1950 meeting. This is the eleventh paper in a series of joint paleobotanical contributions by the above authors. The order of these authors' names is not significant as they are equally responsible for the content of each contribution.

NORTH AMERICAN DEVONIAN PLANT RECORD

Before considering in some detail the flora characteristic of the black shales, a brief resumé of the recorded fossil floras throughout both the Devonian and Mississippian is pertinent. Knowledge of the fossil plants of the Devonian of North America is not extensive. It is based principally on compressions and impressions from eastern United States and Canada and from a number of additional widely scattered localities.

The Lower Devonian flora is best known from the Gaspé and Bay du Nord areas of maritime Canada and from Beartooth Butte, Wyoming. Of the Middle Devonian floras probably the best known is that from the Gilboa, New York, area where casts of rather large trees are found which are probably referable to the genus *Aneurophy-*

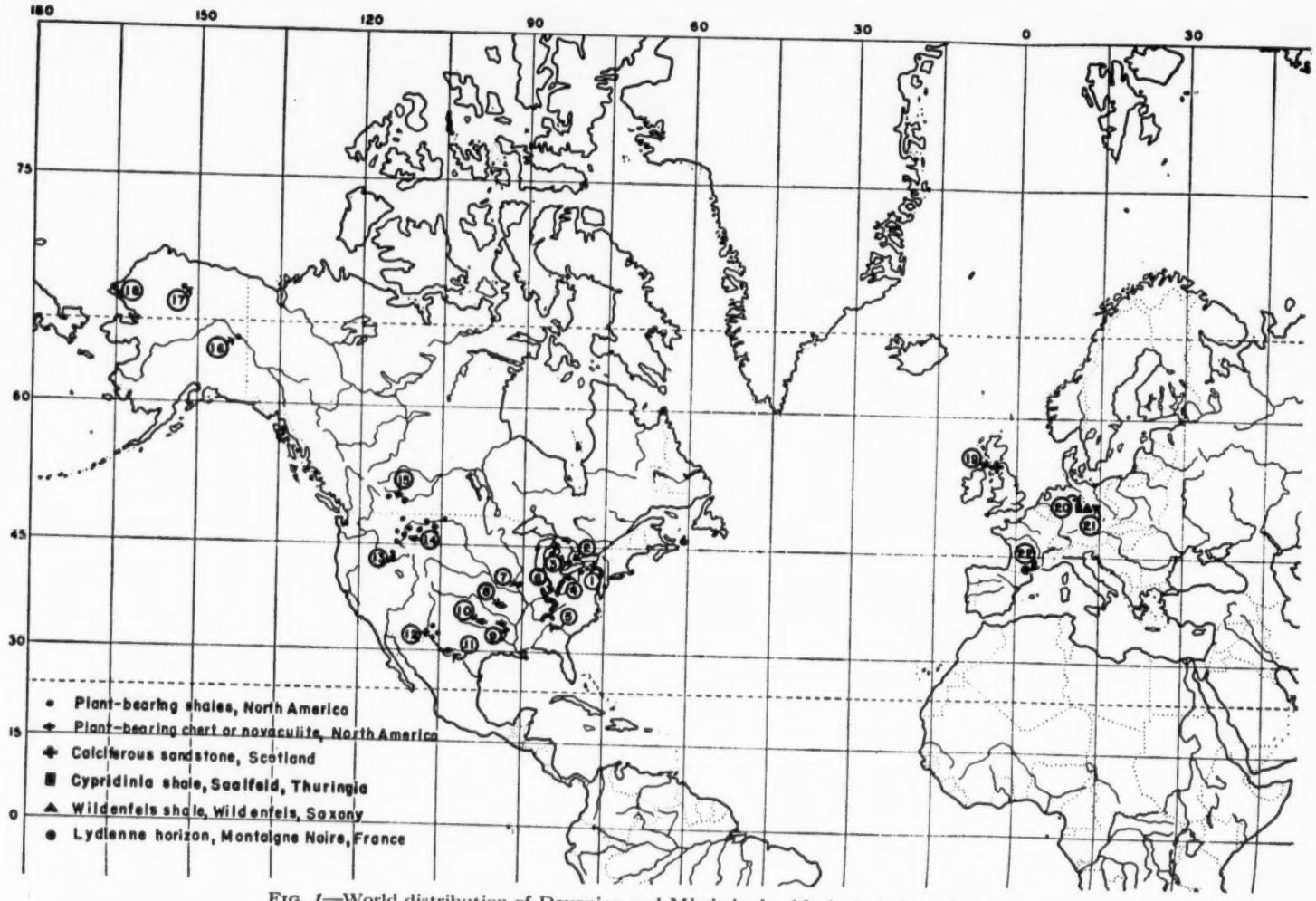

FIG. 1—World distribution of Devonian and Mississippian black shale floras including other similar floras of more or less comparable age.

ton, though originally described by Dr. Winifred Goldring as *Eospermatopteris*. The numerous stumps in the several layers of the Gilboa forest are accompanied by a good compression flora. A less well known petrified flora occurs near the top of the Middle Devonian in the "Tully" pyrite of the Moscow formation. Fragmentary remains are recorded from the Marcellus and the Ludlowville formations.

The Upper Devonian flora is confined principally to black shales. Notable exceptions are occurrences in the Perry Basin of Maine and adjacent areas of New Brunswick and in the environs of Chaleur Bay. Isolated specimens of vascular plants are preserved as petrifactions in the Upper Devonian black shales of eastern United States and in chert and novaculite from Arkansas and Oklahoma which are believed to be their stratigraphic near-equivalents. Practically every zone from the Marcellus to the Pocono has yielded plant remains of one sort or another in the great Catskill delta area of New York and Pennsylvania.

NORTH AMERICAN MISSISSIPPIAN PLANT RECORD

Known collecting localities for Mississippian plants in North America are scattered. The most abundant accumulation of petrified plants, constituting a remarkable flora, occurs in the upper portions of the black shale of early Mississippian age at localities 5 to 7, figure 1. These generalized localities are shown in greater detail in figure 5.

The plant-bearing deposits of earlier Mississippian age in the eastern part of the continent, the Pocono of Pennsylvania, the Price of Virginia and West Virginia and the Horton Bluff formation of eastern Canada, are interpreted as being in part equivalent to the later black shale accumulations and in part to the shales and siltstones underlying the great mid-Mississippian limestones.

The flora from localities 16 to 18 (fig. 1) in Alaska is reported to be early Mississippian in age, though it is quite possibly much younger. A few fossil plants have been reported from the Milligen and Exshaw shale in the Northern Rocky Mountains region but they have not been studied sufficiently to be used stratigraphically.

The paucity of the flora of Middle Mississippian age, especially in the central part of the country, is notable. This is explainable, in part at least, by the widespread limestone accumulation throughout the central and western portions of the country during this part of Mississippian time. An unusually interesting flora, which has been little studied, occurs in Osage strata (lower Middle Mississippian) in southwestern Missouri. This petrified wood is similar to some of that occurring in the Lower Kinderhookian black shales. Abundant floral remains again are known in the United States in the Upper Mississippian (middle and upper Chester), and these are more closely allied to the Pennsylvanian flora, into which they intergrade, than to the earlier Mississippian.

The integration of the floras from the Mississippian is difficult not only because of the very incomplete record of compression specimens, but also because these compression floras are not clearly associated with the less abundant petrified material. Thus it is necessary at present to consider the black shale flora of early Mississippian age as being quite distinct from the older Upper Devonian and from the later Mississippian floras.

STRATIGRAPHY AND DISTRIBUTION OF NEW ALBANY FLORA

Geographic and geologic occurrence.—Figure 2 shows in a very generalized way the distribution of the black shales and adjacent beds of the Upper Devonian and Lower Mississippian in the eastern part of North America. There has been no attempt to divide the Upper Devonian in the New York-Pennsylvania area, inasmuch as there is an intricate assemblage of strata only some of which are black shales, such as the Marcellus and Genesee. The stippled areas adjacent to the black shale outcrop in the east-central interior represent Lower Mississippian strata. The positions of the Nashville and Lexington domes, portions of the Cincinnati arch, are clearly outlined by the black shale outcrops. The black shale crosses the crest of the arch in central Kentucky and northern Tennessee and it may once have extended across the diverging north forks of the arch much closer to the

FIG. 1—World distribution of Devonian and Mississippian black shale floras including other similar floras of more or less comparable age.

FIG. 2—Geologic map showing generalized outcrops of the principal plant-bearing strata of Devonian and Mississippian age, especially the great black shale facies which ranges from mid-Devonian in New York and Pennsylvania (Marcellus *et. seq.*) to early Mississippian (New Albany of Indiana and Kentucky, Chattanooga of Tennessee, Ohio shale of Ohio, Antrim of Michigan and Kettle Point of Ontario). The principal collections have been made along the outcrops from southern Indiana, in central Kentucky, and the west flank of the Cincinnati arch to New York.

Cincinnati area than the present northern Ohio-Indiana outcrop area.

Figure 3 shows the stratigraphic distribution of the black shales and associated rocks and their lithologic continuity across the time boundary between Upper Devonian and Lower Mississippian. The principal information for this chart has been taken from Guy Campbell's (1946) excellent study of the New Albany shale, based on a wide array of evidence drawn from every province of the geological sciences. His conclusions must be regarded with deserved respect.

Divisions of New Albany shale.—The New Albany shale has been divided by Campbell into the Blocher (Middle Devonian), Blackiston (Upper Devonian) and Sanderson, Underwood and Henryville (Lower Mississippian) formations. The Blackiston is in part equivalent to the Ohio black shale (Huron and Cleveland formations), the lower part of the lower Blackiston being considered equivalent to the Olentangy, the upper part to the Huron, and the upper Blackiston to the Olmsted member of the Cleveland shale. There has been some disagreement with this correlation, especially by Wilbert H. Hass (1947), because of evidence furnished by conodont studies, but this problem is outside the scope of the present paper.

The main plant-bearing zone occurs in Campbell's Falling Run member of the Sanderson formation and is sometimes referred to as the "nodule bed." Although it is very thin, varying from 2 to 15 inches, it can be traced for at least 100 miles through southern Indiana and Kentucky. In addition to this principal concentration of petrified plants a second plant-bearing nodule zone, about 1 foot below, occurs in the New Albany area. This is Campbell's "lower nodule bed." The remainder of the Sanderson contains occasional pieces and fragments of plant stems and other vascular tissues embedded in phosphate nodules or enclosed in the black shale.

Some fossil plants also have been found in the overlying Underwood formation, which is a thin, gray shale with a zone of phosphate nodules at the top. Above this lies the Henryville formation which constitutes the top of the New Albany shale. The intricate interrelationships of these three formations may be better understood by an examination of figure 4 which, like figure 3, is based mainly on Campbell's studies (1946). The Henryville is a fissile black shale similar to the Sanderson and Blackiston but no petrified plants have been found in it. Between the Henryville and the New Providence shale and siltstone lie the Jacobs Chapel and Rockford formations, both identified as Lower Mississippian (Kinderhook) on the basis of their good invertebrate faunas. They have not yielded recognizable plant fossils.

The Falling Run member of the Sanderson is a rather persistent unit from about 50 miles north of the Ohio River in Indiana, southward and eastward around the Lexington dome and across the Cincinnati arch at least as far as Junction City, Kentucky, where the specimens of this remarkable flora studied by Scott and Jeffrey (1914) were obtained.

Campbell has excellent evidence, based on both the fauna and lithology, that the Falling Run can be traced as far east as Irvine, Kentucky. There the nodules are embedded near the top of the 18-inch thick Bedford gray shale which directly overlies the Sanderson portion of the Ohio shale. The Bedford is in turn overlain by the Sunbury which also contains phosphate nodules and a zone of abundant *Lingula melie* and *Orbiculoidea herzeri* near the base. Campbell was fortunate enough to find a single excellent piece of petrified wood at Irvine which later became the type specimen of Read's *Steloxylon irvingense*. This specimen occurred in the Sanderson several feet below the Bedford shale.

Figure 4 (lower part) shows that the Falling Run interfingers with the Bedford east of the Cincinnati arch. In the Junction City area the gray shale in which the phosphate nodules occur is considered to be Bedford and not New Providence, which it closely resembles, and the nodules themselves are believed to have been derived principally from the Falling Run (Sanderson).

Another admixture occurs west of the Cincinnati arch and north of the Ohio River. In Indiana the Underwood gray shale disappears southward and the Henry-

FIG. 2—Geologic map showing generalized outcrops of the principal plant-bearing strata of Devonian and Mississippian age, especially the great black shale facies which ranges from mid-Devonian in New York and Pennsylvania (Marcellus *et. seq.*) to early Mississippian (New Albany of Indiana and Kentucky, Chattanooga of Tennessee, Ohio shale of Ohio, Antrim of Michigan and Kettle Point of Ontario). The principal collections have been from southern Indiana and Kentucky and the west flank of the Cincinnati arch in southern Ohio, along the outcrop from southern Indiana to central Kentucky,

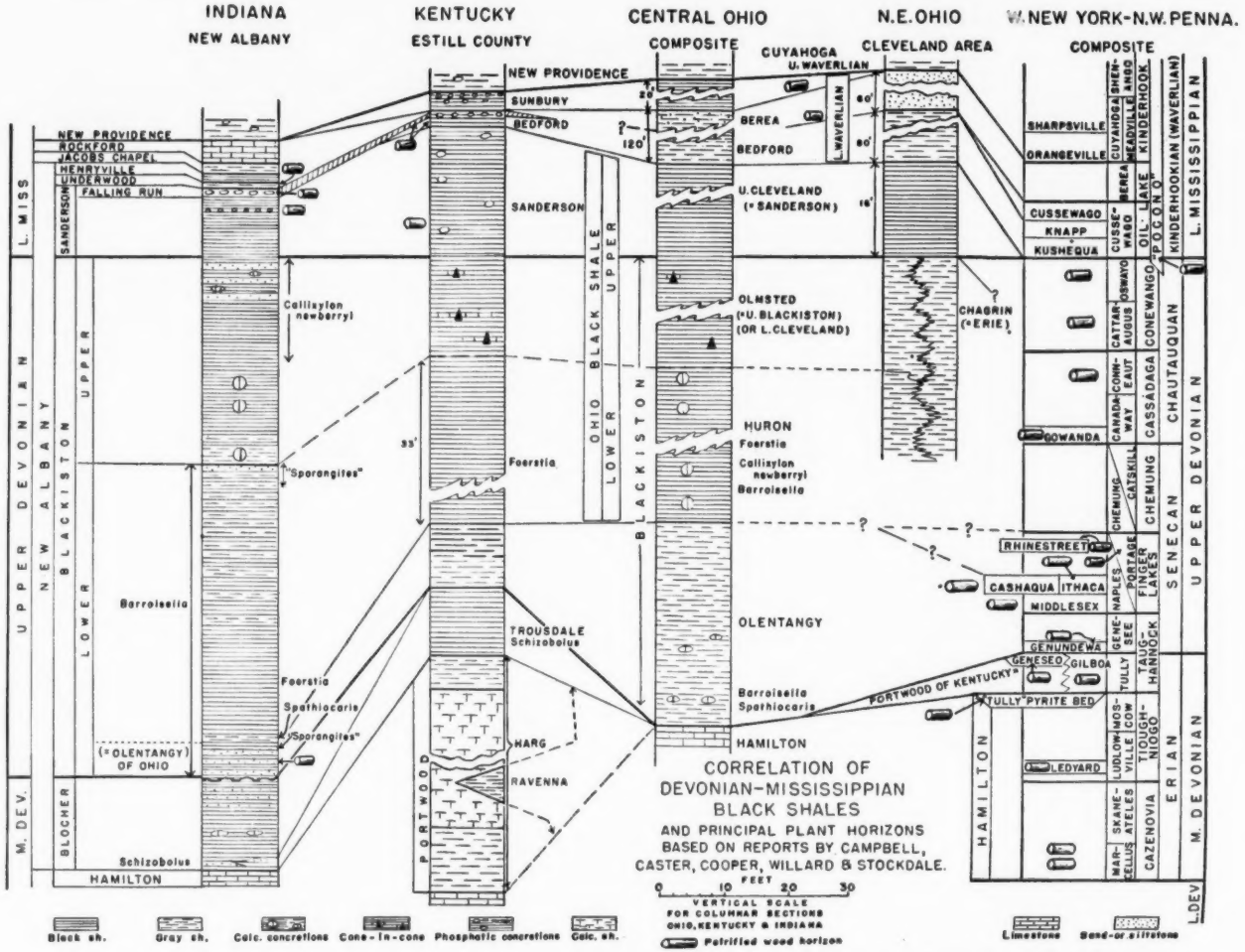

FIG. 3—Correlation of Devonian and Lower Mississippian fossil plant-bearing zones of eastern United States.

ville comes to overlie the Falling Run. Still farther south near the Ohio River the Henryville also feathers out. Although the Underwood thins and/or disappears the phosphate nodules of its upper part persist and become intermixed with the nodules of the Falling Run zone so that it is impossible to tell from which zone the plant remains have been derived unless the nodules also contain characteristic invertebrates.

At the time Scott and Jeffrey first reported their findings from the Linietta Springs locality near Junction City, Kentucky, the time significance of the Falling Run nodule zone was not recognized. The New Providence, which directly overlies the nodule zone at that locality, becomes widely separated from it to the east by northeastward thickening wedges of the Bedford and Sunbury shales (fig. 4). The original report stated that the newly discovered flora is Lower Mississippian in age. Stratigraphically it is considered by Campbell to occur from 10 to 20 feet above the top of the Devonian.

Character and distribution of flora.—The notable flora of the New Albany-Ohio black shale complex is known from petrifactions generally contained in gray shale. The plant fragments appear to be drifted. They also may be preserved in phosphatic concretions or nodules, or they may be isolated fragments scattered through the thinly-laminated black shale. This driftwood type of debris has the appearance of being concentrations of fragmentary organic material which accumulated, along with the phosphatic material, during extended periods of time when sedimentation was very slow. Some of the smaller fragments occur in concretionary masses comprised of intermixed bone, shell and wood fragments in a matrix of spores and spore cases, all phosphatized and strongly suggesting coprolitic aggregation. These concretions of comminuted organic debris have been a principal source of some of the more delicate, small stem or root fragments which have been described from the upper New Albany shale.

The occurrence of these plant fossils is generally restricted to a few inches of shale and phosphatic nodules near the top of the black shale sequence, though a small proportion of them is found scattered throughout the upper few feet (fig. 4). Most of the plant fossils are very difficult to find, their color being almost identical with the matrix of the phosphate nodules. It is necessary to scrutinize the weathered rock and soil painstakingly and examine each possible specimen individually to determine in the field whether or not it is wood.

These plants are accompanied by several types of black shale faunas. Species of *Lingula, Orbiculoidea, Angustidontus, Colpocaris, Spathiocaris, Rhadinichthys, Dinichthys* and numerous conodonts are among those more commonly found.

SOURCE OF NEW ALBANY-OHIO BLACK SHALE FLORA

An abundant flora on the flanks of and across the Cincinnati arch is difficult to explain if no land existed closer than Ozarkia to the west or Appalachia to the east and south. There is some evidence for a nearer source, perhaps a low-lying land area in the vicinity of Cincinnati.

Specimens occur most abundantly high on the arch and become increasingly less common down dip to the east, south and west according to present records. The arc of outcrop from the Junction City-Crab Orchard, Kentucky, area northwest to the vicinity of New Albany has yielded the principal collections. Only a single specimen has been the reward for considerable searching on the east flank of the Nashville dome in Tennessee. Very few have been found in southern Kentucky.

The distribution of *Callixylon Newberryi* logs, which occur throughout most of the outcrop area of the black shales, is not entirely the same (fig. 5, localities 1 to 7, 9, 16, 24, 28, 31, 34, 38, 40 to 42). Even these, however, are found in greater abundance in the same arc of outcrop in southern Indiana and Kentucky. If the logs were transported by rivers of the great Catskill delta to the northeast, or by others flowing westward from Appalachia into a broad, foul inland sea, it is possible that they might have been concentrated for some reason in shallower waters around the Cincinnati arch perhaps by becoming enmeshed in algal mats. This explanation, however, does not account for the presence of exceedingly delicate plant remains, such as stems 2 or 3 mm. in diame-

FIG. 3—Correlation of Devonian and Lower Mississippian fossil plant-bearing zones of eastern United States.

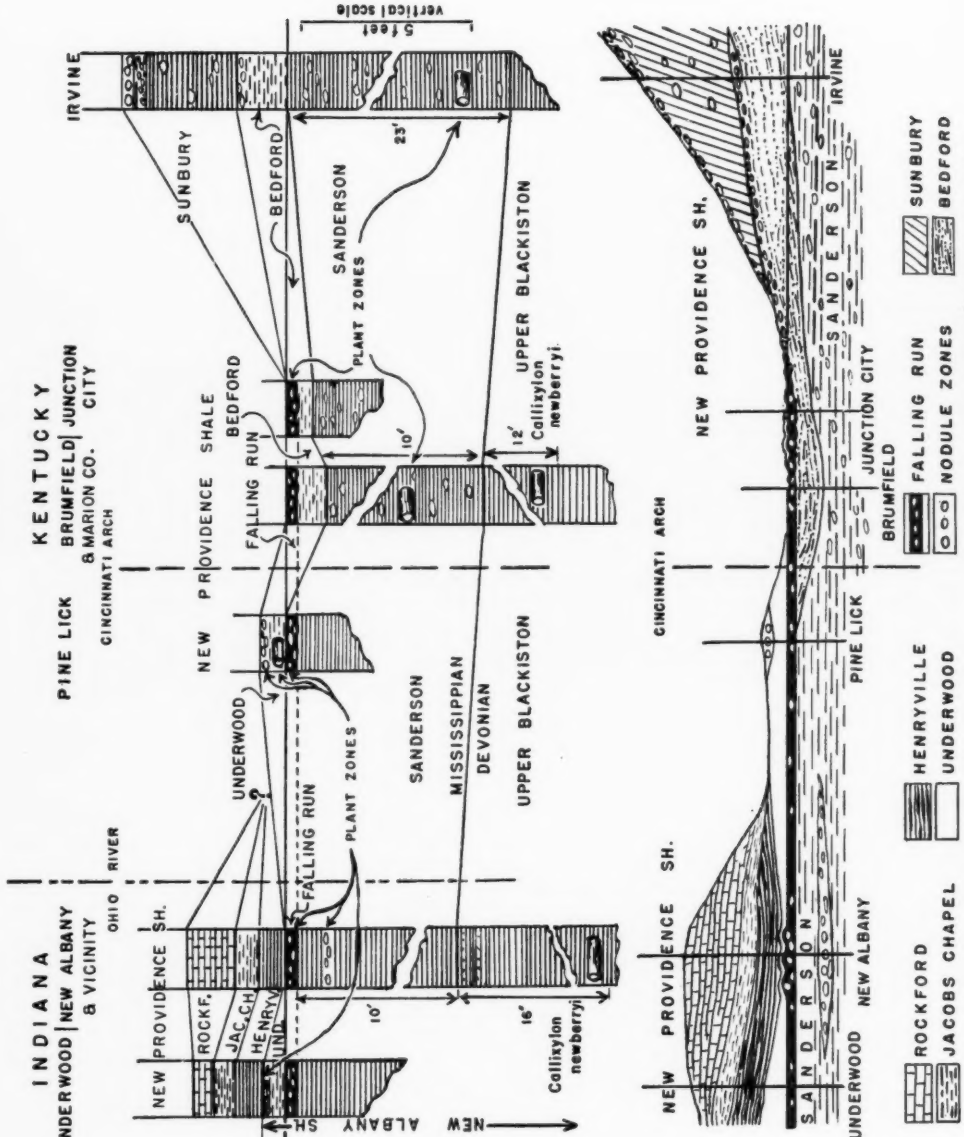

FIG. 4—Correlation of plant-bearing zones of transitional Devonian-Mississippian black shales and associated strata (adapted from Campbell, 1946).

ter, which could hardly have floated such a distance. Perhaps their occurrence in coprolitic nodules suggests a better explanation.

The total lack of leaves in the remains of a great and varied land flora preserved as drifted material in the black shales also is difficult to explain. This may be an indication that the fragments of waterworn wood are far from their source. On the other hand the foul bottom conditions of black shale accumulation probably would be a poor preserving medium for most land plants. The occurrence of algal remains (*Foerstia*, etc.) and highly waxy or resinous spore coats and sporangia suggests that only resistant materials could resist decomposition in such an environment.

FIG. 4—Correlation of plant-bearing zones of transitional Devonian-Mississippian black shales and associated strata (adapted from Campbell, 1946).

FIG. 5—Upper Devonian and Lower Mississippian plant localities of east-central United States. Pertinent locality numbers referred to in text.

DEVONIAN AGE OF BLACKISTON

The New Albany shale is considered, on the basis of its faunal assemblages and lithology, to be a facies which transgresses

the Devonian-Mississippian boundary. The Blackiston formation included within it has been divided into lower and upper parts on the basis of several types of evidence.

Three of the better known plant genera represented in the Blackiston are *Foerstia*, *Tasmanites* ("*Sporangites*" in part) and *Callixylon*. Also occasional pockets and numerous isolated specimens of carbonized plant stems occur throughout the black shale sequence. These have generally been called "strap-like leaves" but thin sections indicate that most of them are slabs or slivers from larger woody masses or smaller flattened branches. They have no stratigraphic value.

Tasmanites is the spore of some primitive plant which must have been extremely abundant during the time of black shale deposition. These spores are generally flattened, disc-like, amber colored and glistening when seen on freshly split shale surfaces but usually darken and become less conspicuous upon exposure and then are easily overlooked. They are variably distributed throughout the black shales and concentrations of them occur at intervals. In the phosphatic nodules they have retained their spherical shape and often are so abundant that they constitute the main mass of material enclosing bone, shell and plant fragments. Their botanical affinity is not certain but they are probably the spores of an alga or some other non-vascular plant. *Tasmanites* is of no index value in subdividing the black shale sequence according to present knowledge.

The thalloid *Foerstia* is a plant of algal nature. Its record is rather clouded by the uncertain identification of some of its immature and unforked forms which have been classified as "*Sporangites*" and *Protosalvinia*. It is usually small and quite dark and probably has escaped the notice of most geologists, but a few of the larger and more conspicuous specimens and better collections have been studied. Its distribution is interesting. Our observations, principally at localities 5, 8, 11, 17 to 18, 29, 31, 41, and 43 to 46 (fig. 5), indicate that it is usually confined to a zone somewhere between one-seventh to one-fifth of the way up in the black shale regardless of the total thickness of those beds. It has been reported from numerous localities in Ohio, Kentucky and Tennessee but many of the earlier records are not precise stratigraphically. There is one record of *Foerstia* (*Protosalvinia*) *ravenna* (White & Stadnichenko) Kräusel, or a closely allied form, in the upper Blackiston in southern Indiana.

Probably the best known of all black shale plants is *Callixylon Newberryi* (Dawson) Elkins & Wieland which normally occurs as segments of large silicified stems embedded in the fissile shale. These stems appear to have floated for some time before sinking into the black mud and are often considerably waterworn. Some are merely slabs from large tree trunks rather than complete boles. They are usually flattened parallel with the bedding of the shale, and the wood sometimes appears to have been considerably decayed before silicification. Crinoids found attached to some specimens also suggest prolonged drifting.

The stems are usually characteristically marked off in rectangular segments by mineral fillings in the cracks or "joints." This mineral stands up in relief on freshly exposed specimens and weathering tends to accentuate the "joints." These cracks appear to have developed from shrinkage without reference to the structure of the wood, which is very homogeneous, dense, and of cordaitalean type. Cracks must have been present before the logs sank and they were promptly mineralized, because thin sections show the logs to be most flattened between them. Evidently the mineralized shrinkage cracks resisted compression in the accumulating sediments more effectively than the less completely mineralized and probably somewhat rotten, soft or watersoaked wood.

At one locality in southern Ohio the *Callixylon* stems are partly silicified and partly calcified and form the nuclei of very large ironstone and calcareous concretions. *Callixylon* probably occurs at many other places in the black shales as part of a multitude of carbonized slabs which are specifically, and for the most part generically, unidentifiable.

Callixylon Newberryi is known from the upper Blackiston portion of the New Albany shale of Indiana and Kentucky and from the Huron member of the Ohio black

shale which is equivalent to the upper part of the lower Blackiston. According to Hass (1947) the entire Blackiston is probably represented by the Huron and, if this is correct, *C. Newberryi* may appear earlier and have a slightly longer range in the eastern region. There are numerous statements or inferences in the literature that this species occurs throughout the black shale sequence but upon investigation this cannot be substantiated. Very few specimens have actually been found in place. Exceptions are those in the Huron concretions of Adams County, Ohio, several specimens from east of New Vienna, Indiana, and one collected near New Albany, Indiana, from the upper Blackiston. Several have been found in streams or low places where their origin from nearby black shale outcrops of determinable upper Blackiston age is reasonably certain. Many specimens cannot be referred to a particular zone with any certainty.

Callixylon Newberryi has been found at a number of localities such as in the Antrim shale of Michigan, the Kettle Point shale near Thedford, Ontario, and from the Ohio, Chattanooga and New Albany shales of Ohio, Tennessee, Kentucky and Indiana, but it is not known to occur above the Devonian-Mississippian boundary. Other species of *Callixylon* have been found in the Mississippian portion (Sanderson formation) of the black shale sequence and these are referred to later. Additional species occur in the Woodford chert of Oklahoma and in the Arkansas novaculite, which are about equivalent in age to the upper New Albany, and also in older strata of New York.

PETRIFACTION FLORA OF SANDERSON

The remarkable variety of woody stems, petioles, cones and roots found throughout the upper portion of the black shale of Lower Mississippian age in the east-central interior is in marked contrast to the paucity of the vascular flora in the Devonian part of the black shale. The scattered distribution of this flora in the lower part of the Sanderson and its concentration in the Falling Run member at the top and in the thin gray shale and nodules of the overlying Underwood formation have been discussed. Its widespread geographic distribution is notable. Phosphatized wood has been collected from 28 localities in Indiana, Kentucky, Tennessee and Illinois (nos. 10, 12 to 15, 17 to 20, 22 to 23, 25 to 30, 32 to 39, and 47 to 49, fig. 5). Some of these are exceedingly small specimens, as little as 2 mm. in diameter and 1 cm. or less in length, but others are as large as limbs or small trees.

About 45 species assigned to more than 25 genera are recorded at the present time (fig. 6). Some of these genera are of questionable identity, others without doubt will be found to be different organs of the same plant. A number of undescribed forms are at hand. The morphology and taxonomy of the major groups represented or of the individual species are not discussed here as these are being studied systematically and some of the results are awaiting publication elsewhere.

Figure 6 shows diagrammatic cross-sections of stems, petioles, roots (?) and strobili of 25 of the principal genera of the New Albany flora represented in the collections. The primitive lycopods and the calamitean groups are poorly represented. However some of the later lycopods such as *Lepidodendron* and *Lepidostrobus* have been found at several localities. Two new species each of *Lepidodendron* and *Lepidostrobus* have been described and at least two more await description. The Cladoxylales, which may be placed systematically somewhere near the ferns, and a few other forms of primitive ferns or plants of fern-like character are known from a number of specimens. A very few stems assigned to psilophytalean genera are at hand. These are too poorly understood to give that group any real significance in characterizing the New Albany flora. At least two orders of early gymnosperms, the Cycadofilicales and Cordaitales, are represented in nearly every collection. The Calamopityeae, the Pityeae and several genera of uncertain affinity must have been prominent components of this flora.

DEVONIAN COMPONENTS OF SANDERSON FLORA

Read (Read and Campbell, 1939), in a report conflicting with the stratigraphic conclusions of Guy Campbell's later extensive work, emphasized the opinion that these

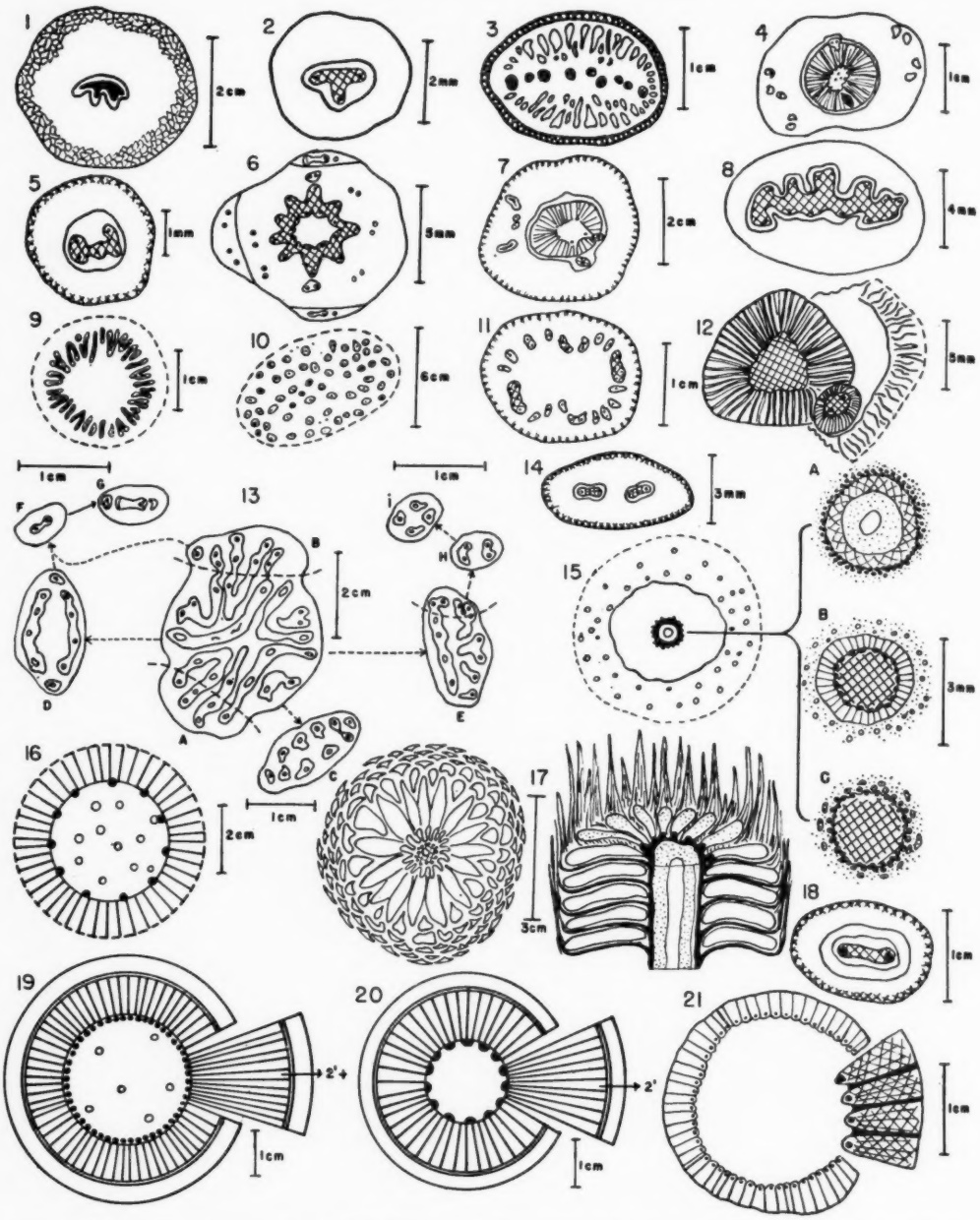

FIG. 6—Diagrammatic cross-sections of the principal genera of fossil woods recorded from the Mississippian portion of the New Albany-Ohio shales. 1, *Microzygia;* 2, *Reimannia* (?); 3. *Periastron;* 4, *Calamopitys;* 5, *Mesoneuron;* 6, *Siderella;* 7, *Diichnia;* 8, *Plicorachis;* 9, *Pietzschia;* 10, *Steloxylon;* 11, *Kalymma;* 12, *Stenomyelon;* 13, *Cladoxylon* and postulated related genera of its branching system; A–E, *Hierogramma* and mode of bifurcation from *Cladoxylon;* F–G, *Clepsydropsis* and origin from *Hierogramma;* H–I, *Syncardia* and origin from *Hierogramma;* 14, *Lyginorachis;* 15, *Lepidodendron,* general tissue orientation of stem; A, *L. boylense* type; B, *L. novalbaniense* type; C, *Lycopogenia* (center of stem only); 16, *Archeopitys;* 17, *Lepidostrobus,* transverse and longitudinal sections of cone; 18, *Stereopteris;* 19, *Pitys;* 20, *Callixylon;* 21, *Protocalamites.*

upper New Albany black shale plants are Devonian in age. This view was based principally on his identification of several genera which he considered as evidence of the Devonian age of the flora or as showing trends distinct from any Carboniferous plants. He cited the following ten genera: *Asteroxylon, Polyxylon, Protolepidodendron, Pietzschia, Reimannia, Siderella, Protocalamites, Microzygia, Periastron* and *Callixylon.*

Three of these genera, *Polyxylon, Siderella* and *Microzygia* are monotypic and known only from the New Albany shale. They have certain primitive anatomical features but it is quite illogical to use them as evidence for dating this flora as they are unknown elsewhere and have no known close relatives.

Two other genera, *Pietzschia* and *Periastron,* are known only from closely comparable strata in Europe. *Pietzschia schülleri,* the only other known species of this genus, was described by Gothan in 1927 on the basis of specimens from the Wildenfels zone in Saxony of controversial Upper Devonian or Lower Mississippian age. The type of petrifaction and the similar nature of the strata suggest correlation with the *Cypridina* shales near Saalfeld in Thuringia from which *Periastron reticulatum* was described by Unger. Another species, *P. delépinei* Corsin, was described from the Lydienne zone near the southern edge of the central plateau of France in the Montaigne-Noire. The flora there, the type of petrifactions, and the strata are all quite similar in many ways to those of the *Cypridina* shales and also the Wildenfels. Of these three localities the Montaigne-Noire is the only one which appears to be dated on faunal evidence as the flora is accompanied by a number of goniatites of Viséan age which provide correlation with the lower Middle Mississippian (Osage) of North America. Thus the New Albany species, *Periastron perforatum* Scott & Jeffrey, *P. reticulatum* Unger and *Pietzschia polyupsilon* Read, cannot be used as evidence of Devonian age because these genera are known elsewhere only from beds of comparable nature and age or from slightly younger strata in Europe.

Another genus, *Protocalamites* (Scott) Lotsy, was cited by Read as evidence of the Devonian age of the New Albany on the basis of the occurrence of a little centripetally developed primary wood. Only one other species is known, *P.* (*Calamites*) *pettycurensis* (Scott) Lotsy, from the Lower Carboniferous Calciferous sandstone series of Pettycur, Scotland. The assignment of Read's species, *Protocalamites dorfii,* to this genus might be strengthened by the study of additional material. A single small specimen discovered by Mr. Campbell consists of a portion of a stem including a node and is clearly calamitean. Granting, however, the occurrence of *Protocalamites* in the New Albany, the only other species is Lower Carboniferous, not Devonian.

Thus six of the ten genera which Read considered evidence for the Devonian age of this flora are limited to the New Albany, or were obtained from beds of doubtful age or from recognized Mississippian strata. The other four genera have been extensively reviewed and the results will be published elsewhere. A summary, however, is given here to complete the analysis of the floral evidence for and against the Devonian age of the New Albany shale.

Genera excluded because of reassignment.— Three of the ten genera mentioned above, *Asteroxylon, Protolepidodendron* and *Reimannia* are generally considered to be Devonian. All species of *Asteroxylon,* except *A. setchelli* from the New Albany, are Devonian. Read believed this genus to be represented by several specimens of at least this one species collected from the Falling Run nodule zone and the lower nodule layer (Read's "plant bed") of the Sanderson formation. The type material of *A. setchelli* is believed by us to be a new genus closely related to some primitive fern.

Read assigned a single specimen from the lower nodule bed to the Devonian genus *Protolepidodendron* on insufficient evidence. Our studies show that this plant is more closely allied with the Cladoxylales, and though the evidence is limited, we believe it cannot be referred to any known genus.

The assignment of a single specimen from the Falling Run member to the Devonian genus, *Reimannia,* originally described by Arnold from the Middle Devonian of New York, must be questioned. Our restudy of the New Albany specimen has not furnished sufficient evidence to warrant its assignment to any known genus and we believe that it

cannot be identified as *Reimannia*.

Sanderson genera with Devonian affinity.—Read has reviewed the early American record of *Cladoxylon* from the Devonian of New York (Dawson, 1882), and has described and figured Clark's specimen as a new species, *C. dawsoni* (Read, 1935). A section of this specimen from the base of the Upper Devonian was examined by Dr. P. Bertrand who, according to Read, was inclined to regard it as a new species of *Cladoxylon*. We have compared this slide with material from the Sanderson and Falling Run of the New Albany shale which Read identified as cladoxylalean and concur in his identification. Thus *Cladoxylon* which has been described principally from Lower Mississippian or controversial Devonian-Mississippian horizons comparable to the New Albany, appears to have at least one late Devonian representative.

Callixylon is known principally from Devonian strata but occurs in the Mississippian of the east-central interior United States and elsewhere. Its occurrence in strata of Mississippian age is confirmed by the recent discovery of specimens from the type area of the Kinderhook, near Kinderhook, Illinois (fig. 5, no. 49) by Dr. Raymond Gutschick of the University of Notre Dame. Numerous specimens of *Callixylon* have been collected from the Sanderson formation at many localities ranging over much of the area of outcrop of the New Albany shale both east and west of the Cincinnati arch and from southern Indiana to the Tennessee state line. Characters of the secondary wood are sufficient to identify this genus (Arnold, 1947, p. 283) and aid materially in differentiating the species, but primary wood is highly desirable for specific discrimination. Because only a few specimens from the Sanderson have primary wood preserved we withhold conclusions concerning the species present. In the manuscript referred to above we present conclusions derived from a study of the type material and other specimens along with a revised description and have reassigned Read's *Pitys brownii* to this genus. A more extensive paper on *Callixylon* from the Sanderson is not yet ready for publication.

C. Newberryi occurs in the New Albany shale and correlative strata of Ohio, Kentucky, Michigan and elsewhere but does not range above the Devonian according to present knowledge. The discovery of *Callixylon* in Lower Mississippian strata does not alter greatly the previously known Devonian range. This does serve, however, as a reason for reconsidering any inferences concerning the age of such strata as the Woodford chert and Arkansas novaculite based on the supposed restricted Devonian range of *Callixylon*.

MISSISSIPPIAN COMPONENTS OF SANDERSON FLORA

Several genera of New Albany plants are represented elsewhere by Mississippian or younger species and three are recorded from strata at least as recent as Upper Carboniferous or Permian. *Lepidodendron* and *Lepidostrobus*, two well known lycopods, need little discussion. The relatively high degree of development of the two species of *Lepidostrobus* cones, *L. kentuckiensis* (Scott & Jeffrey) Scott and *L. noei* Mathews, is notable. They are large, unusually well preserved, and generally similar to the numerous strobili of this genus known from later Carboniferous floras. *L. noei* was originally recorded as probably from either the Upper Devonian or New Providence shales of Kentucky, but after examination of the type specimen and the area from which it came (fig. 5, locality 13) we believe it to have been derived from a horizon comparable to the Bedford shale at Irvine, Kentucky. This specimen is phosphatized and is not calcified as originally recorded. *Steloxylon*, another genus considered to have Upper Carboniferous or Permian representatives, is known by a number of specimens grouped in two species from the New Albany shale. This genus was originally described from a specimen found in redeposited material in the Permian of Siberia whose true age may be considerably older, and range of the genus into the Permian is doubtful. One of the specimens of *Cladoxylon* described from the *Cypridina* shales is generically referable to *Steloxylon* according to Bertrand.

Two other genera which range into Upper Mississippian are *Calamopitys* and *Lyginorachis*. *Calamopitys* was founded by Unger on specimens from the *Cypridina* shales (*C. saturni* Unger). It has since been found in

the Lydienne zone (*C. blayaci* Corsin), the Falling Run-Bedford zone at Junction City, Kentucky (*C. americana* Scott & Jeffrey) and the Calciferous Sandstone (Oil Shale group) of Scotland. Two more species were described from the Lower Carboniferous of Silesia and Hungary and other representatives have been reported from the Carboniferous outside the New Albany shale, one, *L. Papilio* (Kidston) Scott, from the Cementstone group of the Calciferous sandstone series (older Lower Carboniferous of Scotland) and the other, *L. Taitiana* Kidston, from somewhat higher in the Carboniferous limestone series.

The only other upper New Albany genera

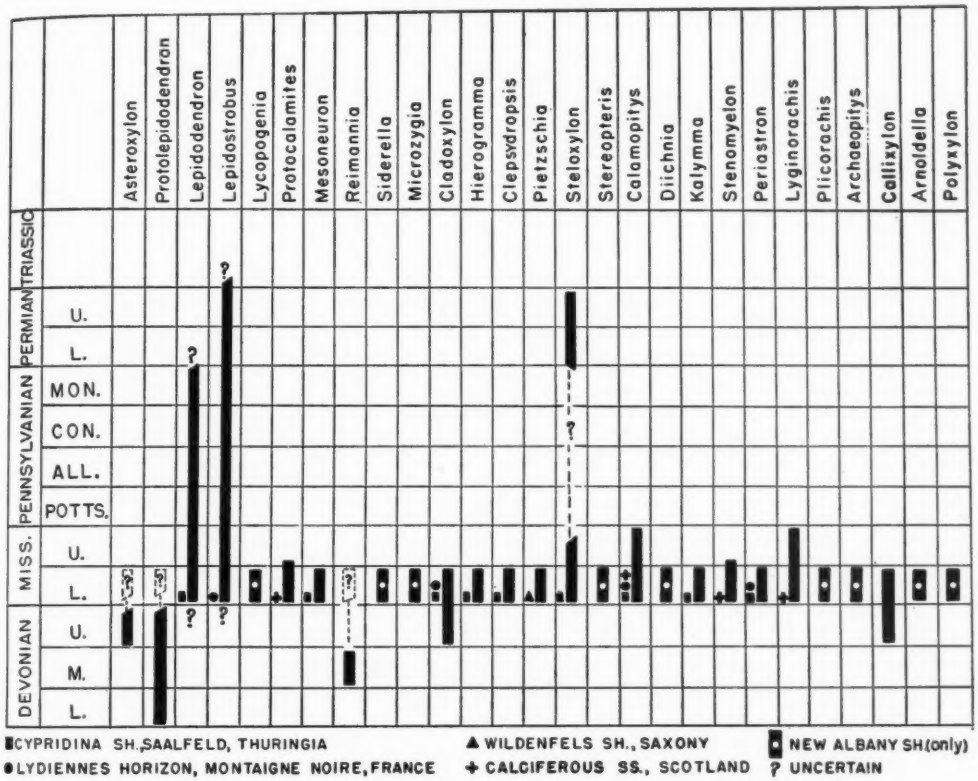

FIG. 7—Stratigraphic ranges of upper New Albany genera and their occurrences in strata of generally comparable age.

iferous limestone series (Upper Mississippian in part) at several Scottish localities. The only record of *Calamopitys* outside Mississippian or Lower Carboniferous deposits or controversial Devonian-Mississippian strata is the species of *Sphenoxylon* (*Calamopitys*) *eupunctata* (Thomas) Read from the Upper Devonian of New York, and Read believed that this species is sufficiently distinct from *Calamopitys* to warrant its assignment to a different genus (Read, 1937, p. 91). *Lyginorachis* is known from two species which have a longer range elsewhere are *Protocalamites*, already discussed, and *Stenomyelon*, a calamopityean ally. The latter is known elsewhere only from the Calciferous Sandstone of Scotland. The precise dating of these specimens, and those of *Protocalamites* from the Calciferous Sandstone, is uncertain but probably they are not younger than upper Kinderhook or lower Osage.

Of the seven New Albany genera known to have younger representatives, two (*Protocalamites* and *Stenomyelon*) are limited to the

Lower Carboniferous, two (*Lyginorachis* and *Calamopitys*) known principally from Lower Mississippian equivalents have one or two species ranging into the Upper Mississippian, two (*Lepidostrobus* and *Lepidodendron*) range at least through the Upper Carboniferous and the last (*Steloxylon*) has a questionable Permian representative.

UNIQUE FLORA OF UPPER NEW ALBANY AND COMPARABLE BEDS

Figure 7 emphasizes the unique character of the upper New Albany shale flora as indicated by the assemblage of genera and their known stratigraphic ranges. Only two genera are known to have Devonian representatives, and one of these, *Cladoxylon*, represented by a single Upper Devonian specimen, is relatively common in the Mississippian black shale flora and other floras of comparable age. The other, *Callixylon*, which occurs throughout the Upper Devonian, is well represented in the black shale flora. Except for it, the upper New Albany flora is set off sharply from that of the Upper Devonian.

Likewise the upper New Albany flora is definitely different, although perhaps not quite as completely, from the better known Mississippian floras. Every New Albany genus whose range extends into the younger Mississippian also is known at one or more other localities from strata comparable in age to the upper New Albany. Approximately two-thirds of all the genera are known only from the black shale flora or, in addition, from one or more of the following localities; the *Cypridina* shale, Saalfeld, Thuringia; Wildenfels shale, Saxony; Calciferous Sandstone, Scotland; Lydiennes zone, Montaigne-Noire, France. These are all more or less equivalents or near-equivalents and are of controversial Devonian-Mississippian age except for the Lydienne zone, whose fauna suggests that it is slightly younger (possibly Osage) and the Calciferous sandstone which probably includes slightly later Mississippian strata.

The Lower Mississippian New Albany flora and its counterparts elsewhere is unique in composition and restricted in stratigraphic range. It is similar to neither Devonian nor Mississippian floras, as these are generally recognized and it does not intergrade with them. Little is known of its antecedents or descendents. It is, however, a distinctive flora of relatively wide geographic distribution and should receive much further detailed study.

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MESOZOIC PLANT MICROFOSSILS AND THEIR GEOLOGICAL SIGNIFICANCE[1]

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ABSTRACT—Present knowledge of Mesozoic plant microfossils, especially the sporomorphs, is limited and their study is still in its descriptive stage. Application of modern anatomical methods and comparison with living members in regard to characters displayed by the epidermis and cuticle have yielded phenomenal results necessitating reclassification of many sterile fronds or permitting refinement of existing classifications to receive new genera and higher categories based on these fossils. Examples are presented of the general usefulness of Mesozoic plant microfossils for stratigraphic work. The need for more intensive collecting and study of more microfossils is demonstrated.

INTRODUCTION

LONG known as the Age of Cycads, the Mesozoic is now more appropriately called the Age of Cycadophytes. This designation records one of the major advances in our knowledge of Mesozoic plant fossils. In fact, progress in Mesozoic paleobotany has been truly astonishing, both in regard to the methods employed and the results obtained, as illustrated by the examples discussed below.

In the main, this progress has concerned two principal divisions of the plant kingdom, the ferns and fern allies and the gymnosperms. As Harris (1949) has pointed out, work on fossil ferns has not produced any major changes in classification, morphological concepts or stratigraphy, whereas "in the Gymnosperms there has been steady but unspectacular improvement of knowledge of the existing orders." Interestingly enough, "nearly all this progress has been made by the study of the cuticle of leaves and reproductive organs—a layer which in the Gymnosperms is remarkably well developed."

When speaking of Mesozoic plant microfossils it is advantageous to define the term microfossil as broadly as possible. The large fossilized logs exposed in the Petrified Forest of Arizona (Daugherty, 1934, 1941) obviously do not seem to meet this definition. Yet their study involves detailed anatomical analysis before the plants can be identified and classified. Paleobotanists are not always as fortunate as in the case of the Petrified Forest. Even if quite small, wood samples and accompanying fragments may be subjected to anatomical study (Bailey, 1933; Hofmann, 1934; Jarmolenko, 1934), but if overlooked in the appraisal of a certain flora, their omission would definitely distort the limited picture. Many microfossils are remnants or parts of leaves, whose state of preservation permits study by new and effective methods, but extensive research on living relatives and their leaf anatomy is a necessary prerequisite. Microfossils in the conventional sense, pollen and spores, are undoubtedly present in many Mesozoic strata, but have hardly been studied and analyzed on a basis comparable to those of the late Paleozoic and Tertiary (Schopf, 1949; Wilson, 1944). Here then is an almost virgin field for future paleobotanical research which is bound to yield unexpected results, for the greatest change in floras occurred in the Mesozoic during the ascent and subsequent decline of the major gymnosperm groups and the appearance and sudden rise of the angiosperms. So far we can see only the dim outlines of this grandiose spectacle. Even if our hopes are occasionally ahead of our accomplishments, we are slowly converging on the common goal, complete knowledge and understanding of that transformation from the old to the new floras.

[1] This paper was part of the Symposium on Applied Paleobotany read before the Society of Economic Paleontologists and Mineralogists at its 1950 meeting.

MESOZOIC POLLEN AND SPORE FORMS

It is frequently convenient to separate "sporomorphs" (Erdtman, 1947) according to size (Thiergart, 1949) into megaspores and microspores and pollen. Megaspores often can be separated from samples by techniques used in the study of Foraminifera, whereas other sporomorphs must be isolated by different methods.

Megaspores assignable to lycopods have been isolated readily and described from various localities and periods as follows: from Hope Island, Spitzbergen, ranging from Upper Triassic to Lower Cretaceous, as *Triletes hopeniensis* (possibly referable to *Isoëtes*) by Selling (1945); from the famous Gristhorpe plant bed (Jurassic) as *Triletes sparassis* and *T. cyttaria* by Miss Kendall (1942); from the upper and lower Estuarine series of the East Midlands (Jurassic of Yorkshire) as *Triletes harrisi, T. sparassis, T. phyllicus, T. richardsoni, T. polysceles,* all of the Section Apiculatae and *Triletes* sp. "A" of Section Laevigatae by Murray (1939) (the accompanying lignite, charcoal, leaf fragments, and microspores have apparently not yet been studied). The 14 species of megaspores described by Harris (1937) from the Rhaetic or the Liassic of eastern Greenland are confined to these strata, as are the larger plant fossils. In Murray's words, "This appears to have established that the value of a megaspore species for fairly fine stratigraphic purposes in the Mesozoic is similar to that of other plant fossils." Miner's (1932) nine new species of *Selaginellites* from Upper Cretaceous coals of western Greenland have since been referred to *Triletes* by Harris (1935).

The earliest fairly reliably identified angiosperm pollen has been found in Jurassic deposits by Erdtman (1948) and Simpson (1937). Simpson's report is based on his discovery of such pollen in Scottish coals of Jurassic age. Erdtman's material was collected from the early Jurassic shale of Palsjö in northwestern Scania and given the abstract name *Tricolpites* (*Eucommiidites*) *Troedssonii* with its concrete name placed in parentheses. Tricolpate pollen of this kind (with three meridional furrows or colpae) according to our present knowledge is characteristic only of dicotyledonous plants. Erdtman's plate shows also an accompanying sporomorph, *Monosulcites magnolioides,* with magnolioid features but probably of gymnosperm affinity, as it somewhat resembles pollen grains of the bennettitalean genus *Wonnacottia.*

The Scottish coals from Brora, Sutherlandshire, studied by Simpson, rest on strata of the Estuarine series. They are rich in pollen belonging principally to the Abietineae and Nymphaeaceae. The pollen of the latter group is readily identifiable by a narrow furrow which is either ring-like or open at one or both ends. The pollen of *Nelumbium* is not trilateral but bilateral, a feature regarded as primitive. The other genus represented is *Castalia,* whereas some other forms not identified resemble *Magnolia* and its allies. Although not as old as the leaf, *Furcula granulifera,* from the Rhaetic of eastern Greenland (Harris, 1932) and the gnetalean (or ?dicotyledonous) wood, *Schilderiana adamanica,* from the Upper Triassic of Arizona (Daugherty, 1934), these Jurassic pollen grains are further evidence of the greater age of angiosperms postulated by Thomas (1947).

Triassic spores and pollen from the Deep River coal field of North Carolina are being studied by Berry (fide Wilson, 1944). Five Triassic spores have been described from the petrified forests of Arizona by Daugherty (1941). The most common of these, *Alisporites opii,* resembles forms found in Greenland and Germany. It has not been referred to any group, as all winged spores are not necessarily identifiable with the Abietineae or Podocarpineae. This spore is commonly parasitized by a chytrid fungus, *Rhizophidites triassicus.* In the southern hemisphere Sitholey (1945) has described various "plant remains from the Triassic of the Salt Range in the Punjab," and Rao (1936a, b) has described winged pollen, spores and sporangia from the Jurassic of India. In a letter Te Punga (1949) has announced forthcoming descriptions of some 75 to 100 sporomorphs from late Cretaceous and early Tertiary coals of New Zealand, including Cretaceous *Nothofagus* pollen. The pollen from the Upper Cretaceous of Namaqualand, South Africa, can be referred to two conifers (Pinaceae) and four angiosperms (*Corylus* and *Myrica*). According to Kirchheimer (1932) these genera do not occur in the present flora of the area.

The principal microspore types of the

Ipswich coals of southeastern Queensland were carefully studied by de Jersey (1949) and classified following Dulhunty's system (1946), the letter *T* indicating their reputed Middle Triassic age. Of the 31 types recognized, 11, or 35 per cent, occur also in the Permian coals of Queensland. On this basis the "Ipswich series may be even older than Middle Triassic, the age suggested by a recent study of the flora (Jones and de Jersey, 1947, p. 82)" (de Jersey, 1949, p. 6).

The largest series, virtually complete, of the pollen and spore contents of Mesozoic strata of one area has been worked out by Thiergart (1949). In his opinion, the Mesozoic microfauna is rather well known, whereas the microflora is practically unknown. The isolated examples given above substantiate this view readily. With the exception of the Middle Cretaceous, Thiergart had samples from all major Mesozoic strata of Germany and Austria. He studied only sporomorphs ranging in size from 10 μ to 200 μ, purposely omitting all megaspores from this analysis. The samples consisted mainly of pteridophyte spores and gymnosperm pollen, as angiosperm pollen of dicotyledonous affinity appears only in the Cretaceous. Monocotyledonous pollen is practically absent, although palm pollen is present at the transition from the Cretaceous to the Paleocene. This is botanically deplorable but stratigraphically unimportant.

Thiergart, like others, found it hard to distinguish between pteridophyte spores and gymnosperm pollen, particularly since either may belong to genera or families now extinct. This difficulty was overcome, in part at least, by the introduction of a new method. Zetzsche and Kälin (1932) had found that pollenin and sporonin differ chemically, provided that neither spores nor pollen are too highly carbonized, or that polymerization has not reached its final stage. Polymerized pollenin and sporonin can thus be distinguished chemically, for they react differently to stains, especially to fuchsin. In a 0.5 per cent alcoholic solution of fuchsin sporonin turns light pink, whereas pollenin turns dark red to purple, and in this way they are easily distinguished. As a group *Lycopodium* spores do not stain at all and in other spores the brown color of the heavy spore coats may conceal the pink stain. Excessive staining is to be avoided. Thiergart referred all sporomorphs which cannot be assigned to either pteridophytes or gymnosperms to *Sporo-pollenites*. Other established form genera also were recognized and new entities described under them. By way of summary Thiergart presented a diagram of the percentages of spores and pollen representative of the various periods and a comparative chart showing the occurrence and relative frequency of each type plotted against locality and geological range. This series is bound to become a standard for future comparisons after more sporomorphs have been studied and added to the present collection.

CUTICULAR ANALYSIS

Elaborating the techniques and methods devised by earlier paleobotanists, (Thomas, 1911, 1930; Thomas and Bancroft, 1913), Harris (1931–1937) used these methods successfully on the beautiful material collected by him in eastern Greenland from the Rhaetic and Liassic deposits of Scoresby Sound. However, the study of cuticles of leaves and reproductive organs, especially those of the various classes of gymnosperms, has made the greatest progress under the leadership of Rudolf Florin (1931, 1933a, b), who applied the results obtained by detailed study of epidermal characteristics of living conifers and other gymnosperms to fossil material, particularly of Mesozoic gymnosperms. The cuticle, a surface structure of the epidermis, is particularly well developed and often well preserved in fossil gymnosperms. Florin tested and classified, in the light of his knowledge of the origin, development, mature form and distribution of the stomatal apparatus and other cuticular characteristics in living forms, numerous fossil leaves and reproductive organs previously disregarded as sterile or misidentified.

The application of this new technique to the study of Mesozoic gymnosperm leaves and reproductive organs has all but revolutionized old conceptions. As Harris (1949) stated,

> The Cycads have been most spectacularly advanced. This group, once supposed to be the dominant Mesozoic family, faded from the picture as one after another "cycad" proved to be a member of the Bennettitales, a very different group which converged on the Cycads in evolution. Now, however, some very common Mesozoic

leaf genera have been shown to have Cycad reproductive organs of modern aspect. The Cycads return as a major Mesozoic group though not quite a dominant one. It would appear also that they are a group which completed their important evolutionary changes very early and then, like Ginkgo, submitted to no further change, but only to death.

In his now classic studies of the epidermis of conifers and other gymnosperms, Florin (1931, 1933a, b) distinguished two main types of stomatal apparatus:

1. Simple type (=haplocheile 1933): original mother cell divides longitudinally and becomes mother of guard cells; lateral cells are epidermal cells equivalent to mother cell or are produced by epidermal cells. (Haplocheile = with a simple lip.) Present in majority of gymnosperms.

2. Advanced type (=syndetocheile 1933)[2]: normally mother cell divides twice, median cell functioning as mother cell of guard cells and dividing longitudinally; lateral cells are thus direct descendants of original mother cell; they function either directly as subsidiary cells or the latter are cut off from them by longitudinal walls. (Syndetocheile = with compound lip.) Found in Bennettitales, Welwitschiaceae, Gnetaceae.

(For details see the original papers with numerous illustrations.)

In conifers the stomatal apparatus provides the most constant epidermal character. Moreover, it is so well expressed in all gymnosperms that it may be used in distinguishing orders. As a result, many sterile fossil leaves have now been properly assigned after cuticular analysis. An elegant example, as worked out by Florin, may be detailed in this connection. Florin attempted a reconstruction of the cycad which is made up of the megasporophyll called *Palaeocycas integer* (Nathorst) Florin from the Rhaetic of Bjuv in Schonen and associated sterile fronds described as *Bjuvia simplex* Florin from the same stratum. The genus *Palaeocycas* is now extinct.

In the same paper Florin created the new genus *Almargemia* for sterile fronds from the Cretaceous of Portugal whose affinity with the Cycadales-Zamioideae is quite probable. These fronds were previously thought to belong to *Ctenidium*, a cycadophyte.

Another interesting example of the usefulness of cuticular analysis was furnished by Miss Hofmann (1948). In her study of flysch deposits from the Upper Cretaceous near Muntigl (Salzburg, Austria), she found various cuticles, wood, pollen and spores, representing a mangrove type of vegetation. Apparently a shallow sea extended along the northern rim of the Alps which was inhabited by a flora similar in its ecology to modern mangroves but of different floristic composition. The fossil mangrove species are clearly related to living ones, except that *Rhizophora Mangle* and *Avicennia nitida* are now confined to the American flora and *Rhizophora mucronata* is a constituent of that of Indo-Africa. Thus a plant community, which is by no means stationary but almost always on the march, has probably as long a history as other types often regarded as primitive, particularly tropical rain forests (Bews, 1927). The spores represented belong to the well known tropical fern genus *Platycerium*. Thus the flysch can now be recognized as representing a fossil mangrove environment. This problem could not have been solved by analysis of the few animal fossils found in these deposits.

Miner (1932, 1935a, b), in his studies of Greenland and Montana coals, found cuticles some of which are gymnospermous although the majority is of angiosperm affinity. Various seeds, sporangia, etc., included in the samples were also identified. On the basis of this analysis he was able to correlate some coal beds at Patoot and Skansen in the Cretaceous of western Greenland.

PLANT MICROFOSSILS AS AIDS IN MESOZOIC STRATIGRAPHY

In addition to the instances related above, the following remarkable examples of the direct applicability of plant microfossils to problems of stratigraphy may be presented. Of the several cases discussed by Rau (1949) one is particularly instructive. Thin sections of Cretaceous rocks from South India contained, in addition to Foraminifera, "plenty of fossil algae." The algae were studied by J. Pia, whose report was issued in conjunction with stratigraphic studies by Rao

[2] For convenience this term might be contracted to "syncheile," as "alloploid" was derived from allopolyploid.

(1936). The rocks investigated belong to the uppermost Cretaceous beds known as the Niniyur group, Trichinopoly District of South India. Study of the sections disclosed the presence of well calcified Chlorophyceae whose frail forms indicate the absence of direct wave action. The presence of many of these fossils suggests that the salinity of this shallow sea, of 10 to 20 fathoms depth, was quite normal. Pia attempted a hypothetical reconstruction of the forms present on the sea floor at the time of deposition of the Niniyur strata. As most of the species found in this assemblage were new they cannot yet be used to assign this flora either to the Cretaceous or Tertiary. Nevertheless, the sequence of the strata will be typical and "will be used to correlate strata in other parts of the earth with those in the Trichinopoly district and thus to fix the geologic age of these foreign sediments."

Other interesting examples are provided by the Mesozoic of Queensland. According to Jones (1949) these deposits are mainly lacustrine and the fossils are "largely of the vegetable kingdom." Although carbonized fossil plants are rare, anatomical studies of epidermis and wood fragments were carried out and correlated as far as possible, since "fossils showing reproductive structures attached to foliage or to wood, or foliage attached to stems, are treasures."

According to Jones, the designation "*Thinnfeldia* flora" for all Triassic floras of the southern hemisphere is very apt because of its comprehensive character. In his own experience of collecting over 6000 specimens from the type area of the Ipswich series he found that over fifty per cent fall within the limits of the genus as usually understood. The simple structure of its epidermis proves that *Thinnfeldia* is a primitive gymnosperm of unknown affinity. The Queensland and South African forms differ in the reproductive organs ascribed to them, for they are detached in the South African members but attached in the Queensland ones. The genus *Stenopteris* is probably closely related to *Thinnfeldia* for it has a very similar epidermis. Its fertile fronds are unfortunately unknown. As these genera were described from European localities, the southern hemisphere representatives are probably generically distinct as is shown by the differences in their epidermis structures. To date the epidermis of the northern members of *Thinnfeldia* is better known than that of its southern representatives. The various Ginkgoales are likewise subdivided on the basis of their epidermal characters. Of seven species present only one fits the living species of *Ginkgo* because of the similarity of its epidermis. Likewise, if the eight recognized Australian species of *Thinnfeldia* distinguished because of differences in size, form and venation, are studied in regard to their epidermal features, five species turn out to have identical epidermis characters and gradational forms are present. Moreover, these "species" lack any stratigraphic significance and the five with identical epidermis are likely to be members of "one very variable species." Obviously more material is needed to resolve the remaining problem.

Despite considerable difference between the Esk and Ipswich floras, Jones concluded that the Esk flora is a different facies of the Ipswich rather than being referable to the Jurassic Walloon as advocated by Walkom. The Esk series is calcareous throughout but the Ipswich is noncalcareous. Jones thought that the "Esk series is the lateral equivalent of the lower portion of the Ipswich Series" and "equivalent to the Khola Stage of the Ipswich Series." The Esk flora contains the conifer *Elatocladus* and has a "greater abundance of species of '*Thinnfeldia*' with large pinnules and of Bennettitales."

As the other Mesozoic floras of Queensland are even less known, their discussion is here omitted. In short, they need considerable study and more collecting before final stratigraphic assignments can be made. The same can certainly be said of other floras of the southern hemisphere.

After more than ten years of study Harris completed his intensive analysis of the Rhaetic and Liassic floras of Scoresby Sound, eastern Greenland. These studies are among the finest in all paleobotanical literature and, because of the wide application of techniques and methods discussed above, they may be detailed here, at least as far as their world-wide significance is concerned. These floras are now among the best known in the entire world and thus provide a standard for comparison. The main result of

Harris' findings may be anticipated by pointing out that the two floras have most genera in common but differ in their species. With the exception of one new alga and four bryophytes, a total of 192 vascular plants was studied and many were described as new. Of these, 43 species are referable to pteridophytes and 149 to spermatophytes. It is obviously impossible to discuss here in any detail the many interesting types. However, some significant data from Harris' own stratigraphic evaluation may be mentioned.

The fossiliferous strata are 90 meters thick and occur in the upper part of the Cape Stewart formation, a fresh water group 175 meters thick, known to be partly Rhaetic and partly lower Liassic. The older Rhaetic strata are referred to as the *Lepidopteris* zone and the younger lower Liassic strata as the *Thaumatopteris* zone. They are separated by a transition zone 5 meters thick which is nearly devoid of fossils. Harris was able to correlate these Greenland floras with those of similar age in Sweden and southern Germany and to show that all belong to one floral region represented by island-like remnants of land that was being submerged during the Rhaetic transgression. Extending his comparisons to include floras of similar age throughout the world, Harris distinguished three main floral provinces, a northern province ranging from Greenland to Japan, a central province of roughly equal extent including Tonkin, China, Pamir, Persia, Mexico and British Honduras, and a southern province including South Africa, Australia, Argentina and possibly India. So far apparently no floras of comparable age have been reported from North America north of the countries named. Although the floras of these provinces are assessed by comparison with the Greenland floras, most of them, especially those of the southern hemisphere, need restudy and careful analysis by methods similar to those applied to the Greenland floras.

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AGE AND ENVIRONMENT: A SURVEY OF NORTH AMERICAN TERTIARY FLORAS IN RELATION TO PALEOECOLOGY[1]

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ABSTRACT—Seven Upper Cretaceous and 25 Tertiary floras have been analyzed with respect to their generic composition. The genera described from each flora have been divided into three clearly defined categories: 1) native genera, now living in the geographic region of the fossil flora, 2) exotic genera, no longer represented in the geographic region of the fossil flora, and 3) genera which are botanically unidentified, extinct or designated as form genera. Statistical representation of each of the three categories in each flora has been determined and quantitative change in the three categories related to geologic age. It is found that there is a close correlation between increasing geologic age and the percentage of "native" to "exotic" genera. The "native" genera in fossil floras, regardless of geographic location, show a gradual decrease between the Upper Cretaceous and the late Eocene and an almost exponential increase between early Oligocene and late Pliocene. The "exotic" element reaches its peak in the late Oligocene and rapidly declines to the late Pliocene. Changing percentages of the three generic components have been interpreted as representing major migrations of plant populations in response to profound climatic changes during the Cenozoic. Relationship between geologic age and the generic composition of Cenozoic floras is proposed as a means of validating the age assignment of continental deposits bearing plant fossils.

INTRODUCTION

WITHIN the past three decades a very extensive literature and volume of knowledge have accumulated concerning the Cenozoic floras of temperate North America and northwestern Europe. Although these studies have been largely regional, both in the temporal and geographic sense, certain fundamental generalizations regarding vegetational history have emerged from the mass of descriptive data. These conclusions, primarily botanical, have significant implications in the solution or clarification of certain geologic problems, more especially those dealing with climatic, paleoecological and physiographic change during the Cenozoic era. It is proposed in this discussion to relate certain of these major vegetational changes which are recorded in continental deposits to their significance as indicators of age, climate and climatic change during the time interval between the Upper Cretaceous and the end of the Tertiary.

A growing suspicion of the basic validity of the paleoecological method has been voiced in recent years by students of modern plant distribution, largely through emphasis on biotypes and ecotypes of variable species, or species whose widespread distribution in diverse habitats provides little basis for evaluating environmental conditions, either today or in the past. However, when viewed in terms of associations of organisms rather than occurrences of individual species it seems evident that the basic assumptions of paleoecology are sound and that, if due regard be given to oversimplification of essentially complex phenomena in the history of vegetation, it is possible to interpret logically past environments as they are recorded in assemblages of fossil plants.

ASSUMPTIONS

It is perhaps necessary to point out that two fundamental premises of paleoecology are subject to careful scrutiny before their acceptance. The first of these is the assumption that organisms in the past had environmental requirements similar to those which they possess today. The second assumption is that a given environment supports a biotic population which is in equilibrium with environmental conditions, and that

[1] This paper was part of the Symposium on Applied Paleobotany read before the Society of Economic Paleontologists and Mineralogists at its 1950 meeting.

this population will show no major change unless there is alteration of the environment. Acceptance of these two premises logically leads to the possibility of reconstructing past environments in some measure of detail by the identification of diverse members of fossil assemblages.

At first glance the two premises appear to deny the operation of organic evolution, whereby organisms vary, diversify and adapt to changing environmental conditions. To a certain extent this is true and necessitates the restriction of paleoecological reasoning, except in its broader terms, to more recent geologic periods, in particular to those of the Cenozoic.

PLANTS AS CLIMATIC INDEXES

Perhaps the most impressive validation of the significance of plants as true indicators of climate has emerged from the study of Pleistocene and post-glacial vegetation. Within the Pleistocene epoch there is abundant geologic evidence of extreme alteration of climate, quite independent of the biological evidence. Correlated with the sequence of climatic changes in glacial and interglacial stages there is now known in some detail a fluctuating biogeographic pattern which affected both plants and animals. There remains little doubt that the environmental influences of the Pleistocene operated more rapidly than biologic innovation, i.e., evolution. Ample evidence, especially from the study of pollen in post-glacial peats, is now available to show that plant populations in temperate and subtropical latitudes have reflected large scale and coordinated geographic shifts in response to environmental changes (Deevey, 1949). The biogeographic patterns in glaciated and bordering areas were therefore determined primarily by geologic processes, both climatic and physiographic. For these reasons, detailed botanical analysis of plant remains in glacial and post-glacial sediments has resulted in a rather precise calibration of climatic changes as well as migrational changes in plant populations. As pointed out by Reid and Chandler (1933) in their comprehensive study of the Eocene flora of the London clay, "Plants have not been able to escape destruction by adapting, but by migration," nor is there any "evidence from the London Clay and the succeeding Tertiary and Pleistocene floras to show any greater degree of adaptability among genera in the past than among the same genera at the present time." The conclusions reached by Reid and Chandler quite aptly state the case of plant paleoecology, viz., that plant populations are true indices of climate provided that it is the bulk of the flora which predicates the climate, not a few exceptions.

If it may be assumed from the preceding arguments that fossil floras provide a valid basis for interpreting past climates it follows that correlation of climate, as revealed by fossil plants, achieves in part the status of stratigraphic correlation based on comparison of species or genera inasmuch as a relationship between geologic time and climatic change is established. However, the correlation of nonmarine sedimentary series, either by paleoecological (i.e., climatic) comparisons or by floristic comparisons are hampered by two intrinsic difficulties: 1) the problems of accurate botanical identification of plant fossils, in particular foliar remains, and 2) the uncertain possibility of special ecological conditions under which the fossil assemblage developed and was preserved. Moreover, climatic zonation, although differing in intensity and geographic limits from that of today, has undoubtedly affected plant populations and hence vegetational zonation throughout geologic time. For these reasons stratigraphic correlations carried over latitudinally separated areas are to a great extent invalidated or unjustified, in the same manner that it would be illogical to correlate the contemporaneous flora of a New England peat bog with that of the swamp forests of the Gulf Coastal plain on the basis of community of species. In the example cited, indeed, if genera rather than species were to be compared, the two floras might seem more nearly contemporaneous!

STATISTICAL COMPARISONS

In an effort to resolve the problem of relating extinct floras to both age and climate by a simple and yet seemingly logical procedure, a statistical analysis has been made of the generic composition of the major Cenozoic floras described from the continental United States. The survey was at-

TABLE 1—GEOLOGIC AND GEOGRAPHIC DISTRIBUTION OF THE FLORAS ANALYZED

No.	Author	Age	Occurrence	No. Genera[1]
1. Woodbine	Berry	Upper Cretaceous	South-central U. S.	31
2. Tuscaloosa	Berry	Upper Cretaceous	South-central U. S.	63
3. Ripley	Berry	Upper Cretaceous	Southeastern U. S.	62
4. Vermejo	Knowlton	Upper Cretaceous	South-central U. S.	37
5. Laramie	Knowlton	Upper Cretaceous	North-central U. S.	44
6. Medicine Bow	Dorf	Upper Cretaceous	North-central U. S.	40
7. Lance	Dorf	Upper Cretaceous	North-central U. S.	44
7a. Lance	Dorf	Upper Cretaceous	North-central U. S.	37
8. Raton	Knowlton	Paleocene	South-central U. S.	64
9. Wilcox	Berry	Lower Eocene	Southeastern U. S.	200
10. Green River	Brown	Middle Eocene	West-central U. S.	108
11. Claiborne	Berry	Middle Eocene	Southeastern U. S.	56
12. Comstock	Sanborn	Upper Eocene	Western U. S.	21
13. Goshen	Chaney	Upper Eocene	Western U. S.	32
14. Jackson	Berry	Upper Eocene	Southeastern U. S.	82
15. LaPorte	Potbury	Upper Eocene	Western U. S.	33
16. Catahoula	Berry	Lower Oligocene	Southeastern U. S.	11
17. Weaverville	MacGinitie	Lower Oligocene	Western U. S.	34
18. Bridge Creek	Chaney	Upper Oligocene	Western U. S.	34
19. Alum Bluff	Berry	Oligo-Miocene	Southeastern U. S.	12
20. Latah	Berry	Lower Miocene	Northwestern U. S.	65
21. Tehachapi	Axelrod	Middle Miocene	Southeastern U. S.	49
22. Calvert	Berry	Middle Miocene	Southeastern U. S.	21
23. Mascall	Chaney	Upper Miocene	Northwestern U. S.	26
24. San Pablo	Condit	Upper Miocene	Western U. S.	23
25. Weiser	Dorf	Mio-Pliocene	Northwestern U. S.	22
26. Remington Hill	Condit	Mio-Pliocene	Western U. S.	22
27. Esmeralda	Axelrod	Lower Pliocene	Western U. S.	11
28. Black Hawk Ranch	Axelrod	Lower Pliocene	Western U. S.	7
29. Mulholland	Axelrod	Middle Pliocene	Western U. S.	30
30. Sonoma	Axelrod	Upper Pliocene(?)	Western U. S.	26
31. Mt. Eden	Axelrod	Pliocene	Southwestern U. S.	16
32. Citronelle	Berry	Upper Pliocene	Southeastern U. S.	14[2]

[1] The number of genera in the flora has been determined by the authors' tabulation of named genera, supplemented by evaluation of the *probable* generic value of the described species of such forms as *Carpolithes, Carpolithus, Carpites, Antholithes, Antholithus, Phyllites* and other form genera.

[2] Includes *Liquidambar* sp., collected in beds of the Citronelle formation (unpublished).

tempted initially as a possible means of determining the age of Tertiary deposits for which orthodox methods of stratigraphic correlations are not possible, viz., floras represented in lignitic deposits by fruits, seeds, wood and pollen and lacking the more familiar leaf impressions on which paleobotanical stratigraphy has so largely depended in the past. The methodology on which this study is based was originally developed by E. M. Reid (1920), in an attempt to date the Pliocene floras of western Europe by relating the changes in species composition to geologic age. This work was unfortunately complicated by the use of geographic floristic elements and was not limited to determining the simple ratio of native to exotic species and the consistent change in this ratio with geologic time. However, it was clearly demonstrated that a remarkably consistent relationship exists between increasing age and the increasing percentage of exotic species in Pliocene deposits. The method set forth was limited, as a means of age determination, to the later Tertiary, more especially to the Pliocene, in view of the fact that very few living *species* of plants are discernible prior to the late Miocene. Subsequent studies of Pliocene floras of western and central Europe have expanded and somewhat modified the data presented by Reid (Mädler, 1939; Szafer, 1946).

The principle established by comparative analysis of fossil floras, however, seems applicable to the whole of the Cenozoic, if genera rather than species are used as units of analysis and comparison. In the present

TABLE 2—GENERIC COMPOSITION OF THE FLORAS ANALYZED

No.	Age	Generic composition by per cent		
		Unidentified or extinct	Identified and exotic	Identified and native
1. Woodbine Sand	Upper Cretaceous	28	39	33
2. Tuscaloosa	Upper Cretaceous	42	25	33
3. Ripley	Upper Cretaceous	53	23	24
4. Vermejo	Upper Cretaceous	49	38	14
5. Laramie	Upper Cretaceous	39	45	16
6. Medicine Bow	Upper Cretaceous	62	18	20
7. Lance	Upper Cretaceous	75	11	14
7a. Lance	Upper Cretaceous	43	38	19
8. Raton	Paleocene	32	48	20
9. Wilcox	Lower Eocene	47	34	19
10. Green River	Middle Eocene	52	32	16
11. Claiborne	Middle Eocene	32	45	23
12. Comstock	Upper Eocene	4	86	10
13. Goshen	Upper Eocene	7	84	9
14. Jackson	Upper Eocene	36	41	23
15. LaPorte	Upper Eocene	27	61	12
16. Catahoula	Lower Oligocene	37	45	18
17. Weaverville	Lower Oligocene	15	59	26
18. Bridge Creek	Upper Oligocene	4	41	56
19. Alum Bluff	Oligo-Miocene	16	42	42
20. Latah	Lower Miocene	26	40	34
21. Tehachapi	Middle Miocene	8	37	55
22. Calvert	Middle Miocene	10	33	57
23. Mascall	Upper Miocene	4	38	58
24. San Pablo	Upper Miocene	9	39	52
25. Weiser	Mio-Pliocene	10	45	45
26. Remington Hill	Mio-Pliocene	0	32	68
27. Esmeralda	Lower Pliocene	18	9	73
28. Black Hawk Ranch	Lower Pliocene	0	14	86
29. Mulholland	Middle Pliocene	3	17	80
30. Sonoma	Upper Pliocene	3	23	76
31. Mt. Eden	Upper Pliocene	0	6	94
32. Citronelle	Upper Pliocene	0	14	86

study the principle has been applied with respect to the generic composition of 32 Upper Cretaceous and Tertiary floras[2] (table 1). In each case the botanical components of the flora have been divided into three distinct categories: a) genera now represented in the existing flora of the geographic region of the fossil deposit (native genera), b) genera now exotic to the geographic region of the deposit, and c) genera which are either unidentified, extinct or designated as form-genera (table 2). The percentage of each of the three categories has been determined with reference to the total number of genera represented in the flora, and separately plotted in a graphic representation (figs. 1, 2, 3). The relationship discernible, therefore, is that between geologic time and the changing ratio or percentages of the three major components of the flora. In order to simplify the analysis and also to attach greater potential significance to the data, the less definitive groups of lower plants such as fungi and algae, and primitive vascular plants and gymnosperms have been eliminated from consideration in each of the fossil assemblages and attention confined to the angiosperms or flowering plants. The fossil floras selected for detailed comparison with their living equivalents occur in widely separated geographic areas, ranging from the southeastern Gulf Coastal plain to the Pacific Northwest and include also the major Tertiary floras of the High Plains and Rocky Mountain region (table 1).

In order to separate "native" from "exotic" genera in each fossil flora the standard of reference has been the existing

[2] Bibliographic references to fossil floras and to manuals of living floras are cited at the end of the paper, not individually in the text.

geographic distribution of genera recorded in manuals of floras of the respective areas. Thus a genus recorded from Wilcox deposits of western Tennessee which today finds its nearest geographic representation as a species in southern Florida is considered an "exotic" element. Conversely, a genus from the same Wilcox locality which is now represented by a living species in the flora of northern Mississippi is considered a "native" genus in the fossil flora. The concept of exotic is therefore regional in relatively restricted geographic terms and applies to genera which are no longer represented by species existing at present in the bordering geographic region of the fossil flora, in the same manner that introduced plants are considered exotic with reference to the native vegetation.

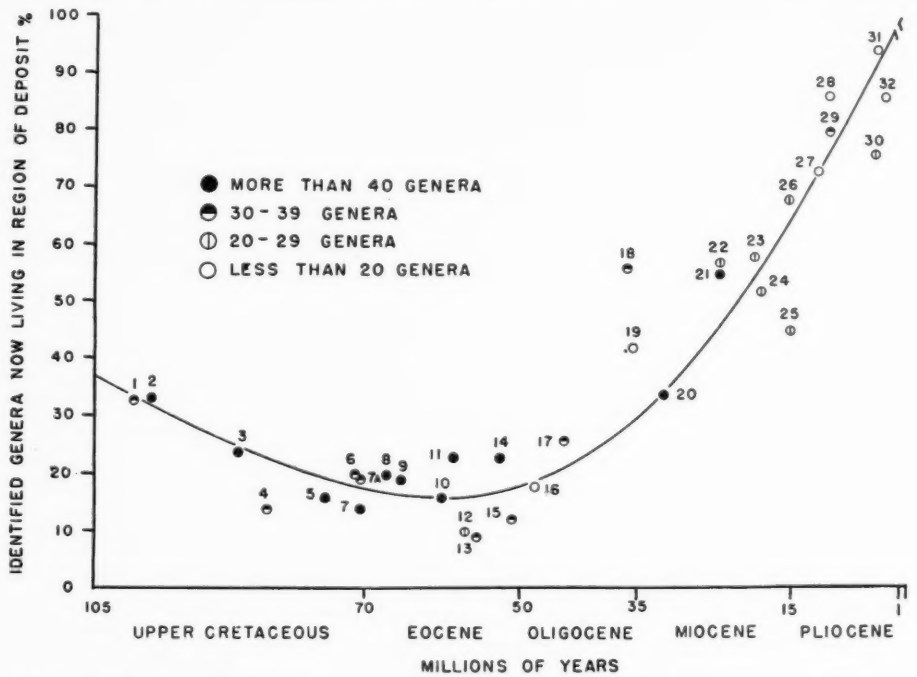

FIG. 1—Graph showing relationship between geologic age and the changing percentage of angiosperm genera in the fossil floras of North America. The data relate percentage of genera in the fossil flora to percentage of the same genera now native to the geographic region of the deposit, and show the changing proportion of native genera during the time interval between the Upper Cretaceous and the Pleistocene. In plotting the data the geologic horizon suggested by the author of each flora has been accepted. Numbers refer to floras listed in tables 1, 2 and 3.

NATIVE VS. EXOTIC GENERA

Examination of the data provided by statistical analysis of the fossil plant assemblages indicates that of the three categories of generic groups the "native" genera prove far more significant than either the "exotic" element or the element of extinct, unidentified or unknown, with respect to consistent change during geologic time (fig. 1). Moreover, it is this "native" element of the fossil flora in which the error of identification is at a minimum, inasmuch as "native" genera are those most familiar to the experience of both botanists and paleobotanists and therefore are most readily identified with accuracy. The exotic element shows a less consistent change in its percentage of representation throughout the Tertiary, although in general these changes are the inverse of those reflected in the changing percentages of "native" genera. That the inverse relationship of native to exotic genera is not more nearly perfect may be explained by the complicating factor of the unidentified or extinct element in fossil floras. The unidentified or extinct element, and it should be

emphasized that we are considering genera rather than species, increases progressively with increasing geologic age, rendering the relationship between these three floristic elements less and less precise in successively older Cenozoic deposits. Additional variation in the data arises from the divergent taxonomic treatment of fossil floras by different authors or by revision of floras by the same author (vide the Lance flora, No. 7 and No. 7a, tables 1 and 2). Discrepancies arising from these causes, however, appear not to invalidate the major conclusions, which have been arrived at by synthesis of numerous investigations of floras of very diverse age, geographic occurrence and botanical affinity.

Statistical analyses of population changes in fossil assemblages are subject to certain inevitable weaknesses in logic. One of these difficulties arises from the misidentification of certain elements in extinct floras and faunas, resulting in errors which are often long perpetuated in the literature. Another arises from the necessity of accepting, only too frequently, circular arguments as to the chronologic position of fossil assemblages in the time sequence. Both of these weaknesses are inherent in the data presented here, but, on the other hand, both are greatly mitigated by the methods used in this composite analysis (table 3). First, genera rather than species have been used as units of extinct populations. This larger and less disputable taxonomic category is far less susceptible to mistaken botanical identification and to misinterpretation than is the species. In the second place, comparative analysis of the floras is not achieved by means of stratigraphic correlation but by direct comparison

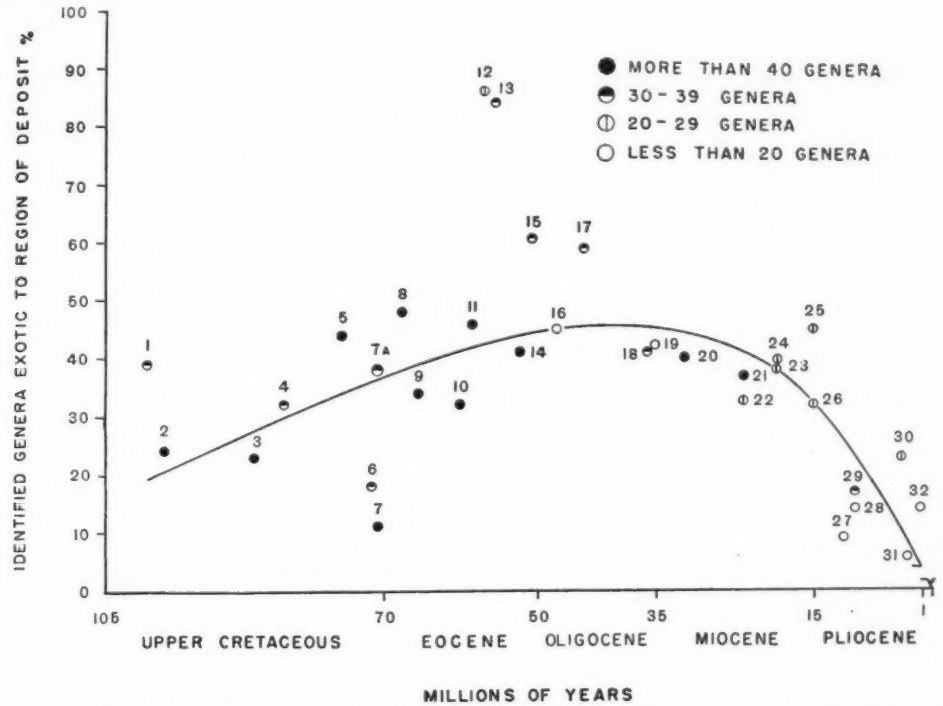

FIG. 2—Graph comparable to figure 1 but showing the changing percentages of exotic angiosperm genera in major fossil floras of North America between the Upper Cretaceous and the Pleistocene. The exotic element is composed primarily of genera now limited to warmer temperate or subtropical regions as compared with their geographic occurrence in fossil floras. Note that the highest percentage of exotic genera occurs during the Oligocene and rapidly declines during the Miocene. That the curves shown in figures 1 and 2 are not perfectly reciprocal is probably due in large part to the unidentified generic element in each flora and also to the evolution of new genera which are not recognizable in earlier Tertiary floras. Numbers refer to floras listed in tables 1, 2 and 3.

with an absolute control which is presented by the occurrence and distribution of genera in the living flora. The procedure, therefore, is concerned basically with determining the percentage of deviation from the living flora represented by genera in fossil floras. The fact that a correlation between living and fossil plant assemblages yields a uniformly consistent relationship with geologic time indicates that the interpretation of paleoecologic change resulting from climatic and physiographic change is a reality of the past and not the fortuitous product of translating morphological observations into mathematical data.

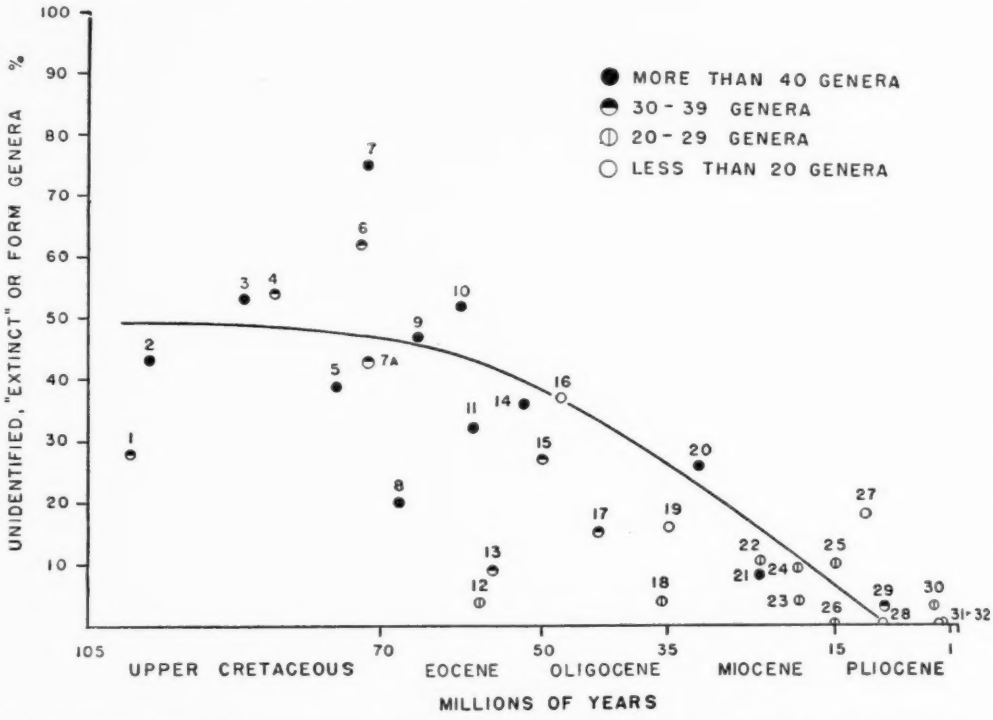

FIG. 3—Graph comparable to figures 1 and 2 but showing the changing percentage of the unidentified or "extinct" angiosperm genera in major fossil floras of North America in the time interval between the Upper Cretaceous and the Pleistocene. Note that this generic element is highly variable, fluctuating both with geologic age and on the taxonomic treatment given by various authors, but is very consistently reduced in extent in later Tertiary floras. Numbers refer to floras listed in tables 1, 2 and 3.

CONCLUSIONS

In time perspective our review of the shifts in generic composition of Tertiary floras shows that the large exotic element of the earlier Tertiary, represented primarily by American subtropical and tropical genera consistently increases from the Upper Cretaceous through the Eocene and early Oligocene. From the early Miocene on there occurs a rapid and accelerating loss of the exotic element, and, pari passu, a rapid and accelerating trend toward the "native" generic composition of the existing flora. The increase of native genera in the later Tertiary shows an almost exponential rate of change, the result probably of accelerating rates of plant migration during the later Tertiary.

Perhaps the most interesting by-product of this comparative analysis of Tertiary floras is the possibility of applying the same statistical method to problems of dating continental deposits for which paleontological evidence is largely limited to fossil plants. It seems evident that within reasonable limits the generic composition of a flora

TABLE 3—EVIDENCE FOR AGE ASSIGNMENT OF FLORAS ANALYZED (AS PROPOSED BY THE RESPECTIVE AUTHORS)

Flora	Paleobotanical correlation and comparison	Stratigraphic and structural (non-paleontological)	Associated vertebrate faunas	Associated invertebrate faunas
1. Woodbine	×	×	—	—
2. Tuscaloosa	×	—	—	—
3. Ripley	×	—	—	—
4. Vermejo	×	×	—	×
5. Laramie	×	×	—	—
6. Medicine Bow	×	×	×	×
7. Lance	×	×	×	×
8. Raton	×	×	—	—
9. Wilcox	×	×	—	×
10. Green River	×	×	×	×
11. Claiborne	×	×	—	—
12. Comstock	×	×	—	×
13. Goshen	×	×?	—	—
14. Jackson	×	×?	—	—
15. LaPorte	×	×	—	—
16. Catahoula	×	—	—	×
17. Weaverville	×	—	—	—
18. Bridge Creek	×	—	—	×
19. Alum Bluff	×	—	—	×
20. Latah	×	—	—	—
21. Tehachapi	×	—	×	—
22. Calvert	×	—	—	×
23. Mascall	×	×	×	—
24. San Pablo	×	—	—	—
25. Weiser	×	—	—	—
26. Remington Hill	×	×	×	×
27. Esmeralda	×	—	×	—
28. Black Hawk Ranch	×	—	×	—
29. Mulholland	×	×	×	×
30. Sonoma	×	—	×?	—
31. Mt. Eden	×	—	×	—
32. Citronelle	×	×	—	×

is a function of age. This relationship seems to be more expressed in post-Eocene rather than Eocene or Cretaceous assemblages, and provides a convenient, although admittedly not precise corollary line of argument for age assignment. The method, however, obviates certain of the more annoying problems of stratigraphic correlation inasmuch as it makes possible, in a very practical way, to establish the correlation of floras containing totally dissimilar categories of plant remains. Problems inherent in correlating floras represented only by leaf impressions with floras represented almost entirely by fruits, seeds, pollen and wood are hence in large part resolved by comparative analysis of their generic geographic relation to living flora. Statistical analyses of generic components in chronologically and geographically separated floras clearly indicate a consistent trend in plant migration during Cenozoic time, the quantitative and qualitative aspects of which are consistent with the interpretation of Tertiary biogeography and paleoecology deduced from the study of fossil floras.

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ONTOGENY OF *BEYRICHIA JONESI* BOLL

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ABSTRACT—A statistical study of valve length in the ostracode, *Beyrichia jonesi* Boll, from the Silurian of Gotland suggests the occurrence of 11 growth-stages in this species. The growth factor appears to be fairly constant (1.28) in all moults except the last. The three youngest stages have been found in the brood pouches of adult females. The orientation of the beyrichids still remains an open question. The microstructure of the shell in *B. jonesi* and some related species is described. The relationship of the beyrichids to recent ostracodes is discussed.

ACKNOWLEDGEMENTS

THIS study was suggested to me by Dr. I. Hessland of Uppsala. It was begun in 1948 at the Natural History Museum in Stockholm where all measurements and most of the photographs were made, and it was continued and finished at the University of Oslo.

I have had the valuable advice and guidance of Professor E. Stensiö in Stockholm, to whom I am indebted for the loan of the specimens studied. I am also deeply grateful to Professor J. Marvin Weller of The University of Chicago and to Professor L. Störmer and Curator G. Henningsmoen of The University of Oslo for their friendly advice, and for criticizing the manuscript.

PREVIOUS WORK

Ostracodes, like most arthropods, grow discontinuously. The calcareous valves are cast off at intervals and replaced by new and larger ones. Some paleontologists have disregarded this fact and described immature specimens as species different from the adults.

So far as I know, Vervorn (1886) was the first to report growth stages in fossil ostracodes (*Beyrichia* from the drift of northern Germany). Kellet (1933) noted the occurence of immature valves and recognized the possible presence of several growth stages. Cooper (1945) described in detail the growth stages of a Pennsylvanian ostracode, and LeRoy (1945) studied the growth stages of Tertiary specimens. Hessland (1949) described and figured many immature stages from the Lower Ordovician of Sweden, and Sohn (1950) has discussed the growth of fossil ostracodes.

The growth of recent ostracodes is much better known. The existence of growth stages was discovered relatively early, and their number and morphology were studied in detail by Müller (1894), Claus (1872, 1894) and others. Fowler (1909) found a relation to exist between the lengths of the valves in the different stages, and similar relations appear to occur also in other groups of crustaceans. Based on the measurements made by himself and others he applied Brooke's law as follows: "During the early growth, each stage increases at each moult by a fixed percentage of its length, which is approximately constant for the species and sex" (Fowler, 1909, p. 224). The lengths of successive stages, therefore, form a geometrical series:

$$L_n = L_1 k^{n-1}$$

where k is the growth factor, L_1 the length of the first stage, and L_n the length of the n-th stage. The value of this law has been further substantiated by the studies of Skogsberg (1920).

The growth factor is usually about 1.25. Przibram (1931) concluded that moulting in the arthropods occurs when the volume of the body has doubled. Thus the growth factor should be 1.26 ($\sqrt[3]{2}$).

Sohn denied both Przibram's conclusions and the applicability of Brooke's law. He seems to have based his calculations on data from several authors (Sohn, 1950, table 1,

p. 430). Very few ostracode students have had enough material for a statistical treatment, and most measurements recorded in the literature come from one or a few specimens only. This may explain some of the deviations from the values calculated according to Brooke's law. Easily detected errors occur in those cases where one stage is missing (growth factor: $1.25^2 = 1.59$), or where one stage is reported twice (growth factor: $1.25 = 1.11$). Only Skogsberg (1920) and Cooper (1945) seem to have had enough specimens for such treatment. Their results are in much closer accordance with Brooke's law than are those obtained from the less complete data of most authors.

My observations neither prove nor disprove Przibram's conclusions, but the fact that the mean growth factor, calculated from the most satisfactory measurements, ranges between 1.21 and 1.29 may be considered distinctly favorable.

Taken strictly, Brooke's law can only be applied to the immature development of an individual up to the stage when it becomes sexually adult. Between possible later moultings the growth is considerably slower than during the earlier development.

The growth rate and the final size of individuals also depends on ecological factors, such as temperature and food supply as known from Recent ostracodes and other crustaceans (e.g., copepods). A species, therefore, has no absolutely fixed growth rate and this may be expected to vary within certain limits with sex and between different populations. Also the growth factor of the last moult differs from the mean of the preceding ones. As mentioned by Skogsberg (1920, p. 147), Brooke's law can be accepted in general, but not without reservations.

MATERIALS AND METHODS

In order to obtain reliable information on the moulting of fossil (and Recent) ostracodes, it is necessary that all the specimens studied be from as nearly the same population as possible. The number of specimens must be sufficiently great to minimize errors that are likely to occur in connection with statistical treatment. The population should be unaccompanied by related species with similar young specimens. No important ecological changes must have taken place during the interval represented by the fossiliferous layer. This last is very difficult to prove, but fossils which may have been redeposited should be avoided. If these precautions are observed, fossil material has one distinct advantage over living specimens. Among the fossils one may expect to find the remains of all stages of development and there is opportunity to compare the relative number of young and adult valves. Because some individuals died before reaching maturity, one may expect to find a relatively smaller number of adults.

Investigations showed that it is extremely difficult to find a "pure" population of fossil ostracodes. Numerous highly fossiliferous marls from the Silurian of Gotland were examined for the most common species, which proved to be *Beyrichia jonesi*. Only a few samples contained sufficient complete, undamaged specimens for statistical treatment. Among these, only one showed no evidence of redeposition. It came from the Mulde marl (uppermost Wenlock) in the Mulde Tegelbruk (brickworks). In this sample adult specimens of other species of *Beyrichia* are practically absent, constituting less than 0.2 per cent of the number of specimens of *B. jonesi*.

Specimens from a few other localities have also been measured: 1) Snäckgärdet, Visby—uppermost Llandovery or lowest Wenlock (*B. jonesi* and *B. spinigera*), 2) Kvarnberget, Slite—middle Wenlock (*B. jonesi*). These measurements are shown graphically in text-figure 2 B–D.

The methods of cleaning and measuring the fossils were very simple. The marl was washed and the fossils picked out under a binocular microscope. All undamaged specimens of *B. jonesi* were mounted on graph paper with squares, 5×5 mm., and measured with an ocular micrometer (1 unit $= 1/35$ mm.). The rows were measured both in horizontal and vertical order, and if the two values for each specimen differed by more than one unit, the measurements were repeated and corrected. The length measured is the greatest length parallel to the hinge line. Spines and fringes were disregarded. The plotting of the measurements is similar to that of Skogsberg (1920) for recent ostracodes. Text-figure 2A shows the measurements of 972 valves from the Mulde

population. All complete specimens with both valves in natural position were counted as two valves.

Growth stages are distinctly separable only if variation within a single stage is smaller than the difference in length between one stage and the next. Otherwise measurements overlap and it may be impossible by the length alone to determine to which stage all valves belong. Several very distinct size groups are obvious in the Mulde population (text-figure 2A) and no overlapping was found. Therefore it seems safe to conclude that these groups represent different stages in the development of *Beyrichia jonesi*.

The stages are numbered consecutively, 1 for the first and 11 for the last. This terminology, however, may not be correct because both the first and last stages are somewhat doubtful but it is currently employed by most zoologists and seems most useful.

The morphological terms used in this paper are largely those of Triebel (1941) and Hessland (1949), and are explained in text-figure 1.

MOULT STAGES OF *Beyrichia Jonesi*

Text-figure 2A clearly shows that specimens of the smaller stages are most abundant and that the range of size variability increases in successive stages, as might be expected. The most important measurements of the Mulde population are shown in table 1. Table 2 presents the data on other populations from Gotland. In table 3 previously published data on fossil and Recent ostracodes are shown. For the sake of comparison the data of table 3 have been recalculated.

Calculations were made by slide rule and consequently are not quite exact but the errors are smaller than the errors of measurement and can be disregarded.

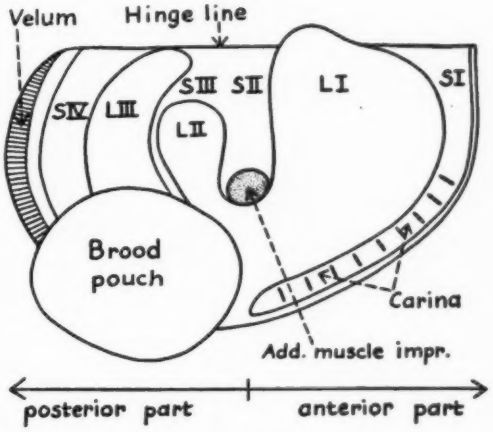


FIG. *1*—*Beyrichia jonesi* Boll. Sketch illustrating morphological terms. LI = anterior lobe, LII = median lobe, LIII = posterior lobe. SII, SIII and SIV are the corresponding sulci.

Table 1 suggests that the growth factor is nearly constant for all moults except the last. The variation (1.4 per cent) in the growth factor of the eight moults recorded in

TABLE 1

STAGE	Number of valves	Length in mm.	Growth factor	Loss in per cent	Complete number	Specimens per cent
11	19	2.171			2	21
10	42	1.914	1.14	55	1	4.5
9	70	1.515	1.27	40	0	0
8	75	1.185	1.27	6	1	2.5
7	92	0.927	1.28	19	4	8.5
6	146	0.728	1.30	38	6	8
5	210	0.571	1.27	33	10	9.5
4	309	0.443	1.29	32	53	34
3	17*	0.343	1.29	—	5	59
2	—*	0.269	(1.29)	—	—	—
1	—*	0.214	(1.26)	—	—	—

Mean growth factor (2:3 to 9:10) = 1.2825 ± 0.0175

* Free specimens only.

TABLE 2

STAGE*	*B. jonesi*, Visby		*B. jonesi*, Slite		*B. spinigera*, Visby	
	Length (1 unit = 1/28 mm.)	Growth factor	Length (1 unit = 1/28 mm.)	Growth factor	Length (1 unit = 1/28 mm.)	Growth factor
11	50.5 ± 7.5	1.275	56.7 ± 7.0	1.205	60.2 ± 5.2	1.245
10	39.5 ± 2.5	1.22	47.0 ± 3.0	1.24	48.5 ± 6.5	1.27
9	32.5 ± 4.5	1.38?	38.0 ± 3.0	1.245	38.2 ± 3.2	1.34?
8	23.5 ± 2.5	(1.28)	30.5 ± 3.5	—	(28.5 ± 3.5)	—
7	(18.3)					
Mean growth factor	1.288 ± 0.092		1.230 ± 0.025		1.285 ± 0.055	

* Assuming 11 growth stages.

the table (2:3 to 9:10) is less than the calculated error of measurements, one unit of 1/35 mm. (1.3 per cent to 8.2 per cent). The smaller growth factor of the last moult may result from the attainment of sexual maturity at this stage. Mature specimens are relatively broader than the younger ones, and if body volume were doubled, increase in length would be correspondingly less. The development of brood-pouches in the females might also influence the relative proportions.

Stage 1.—The maximum length observed in sections is 0.21 mm. The valves are very thin and without sculpture (pl. 103, fig. 1). Only a few specimens have been found and they seem to be so different from the later stages that their identity might be uncertain if they were not contained in the brood pouches of characteristic adult females. This and the succeeding stage are known only from brood pouch sections both as single valves and complete specimens. Stage 3 has been found both in the pouches and free. About 60 adult females from Mulde were sectioned and nearly half contained larval valves. Often several young occur in one brood pouch, and occasionally valves of different stages were found in the same adult individual. Similar occurrence of young individuals living and moulting within the pouches of the mother is known in Recent ostracodes (e.g., Scherer-Ostermeyer, 1940), but was first described from fossil specimens by Hessland (1949, pp. 124–125, pl. 14, fig. 9).

Stage 2.—(pl. 103, fig. 1.) The maximum length observed is 0.27 mm. Because speci-

TABLE 3

STAGE	Cooper, 1945 *Ectodemites plummeri*		LeRoy, 1945 *Cythereis simensis*		Claus, 1872 *Cypris ovum*		Schreiber, 1922 *Cyprinotus incongruens*	
	Length	GF	Length	GF	Length	GF	Length	GF
9	725.0	1.18	1.18	?1.31	0.60	1.11(!)	1.6	1.59(!)
8	618.7	1.16			0.54	1.20	1.008	1.26
7	531.2	1.20	0.90	1.32	0.45	1.28	0.80	1.32
6	446.9	1.22	0.68	1.26	0.35	1.30	0.608	1.23
5	368.4	1.22	0.54	1.21	0.27	1.19	0.496	1.35
4	300.0	1.18	0.45	1.28	0.23	1.21	0.368	1.28
3	253.1	1.225	0.38	—	0.19	1.15	0.288	1.15
2	206.2	1.24	—	—	0.165	1.25	0.25	1.31
1	168.7		—		0.132		0.19	
Mean growth factor	1.21 ± 0.05		1.275 ± 0.065		1.21 ± 0.10		1.31 ± 0.28	

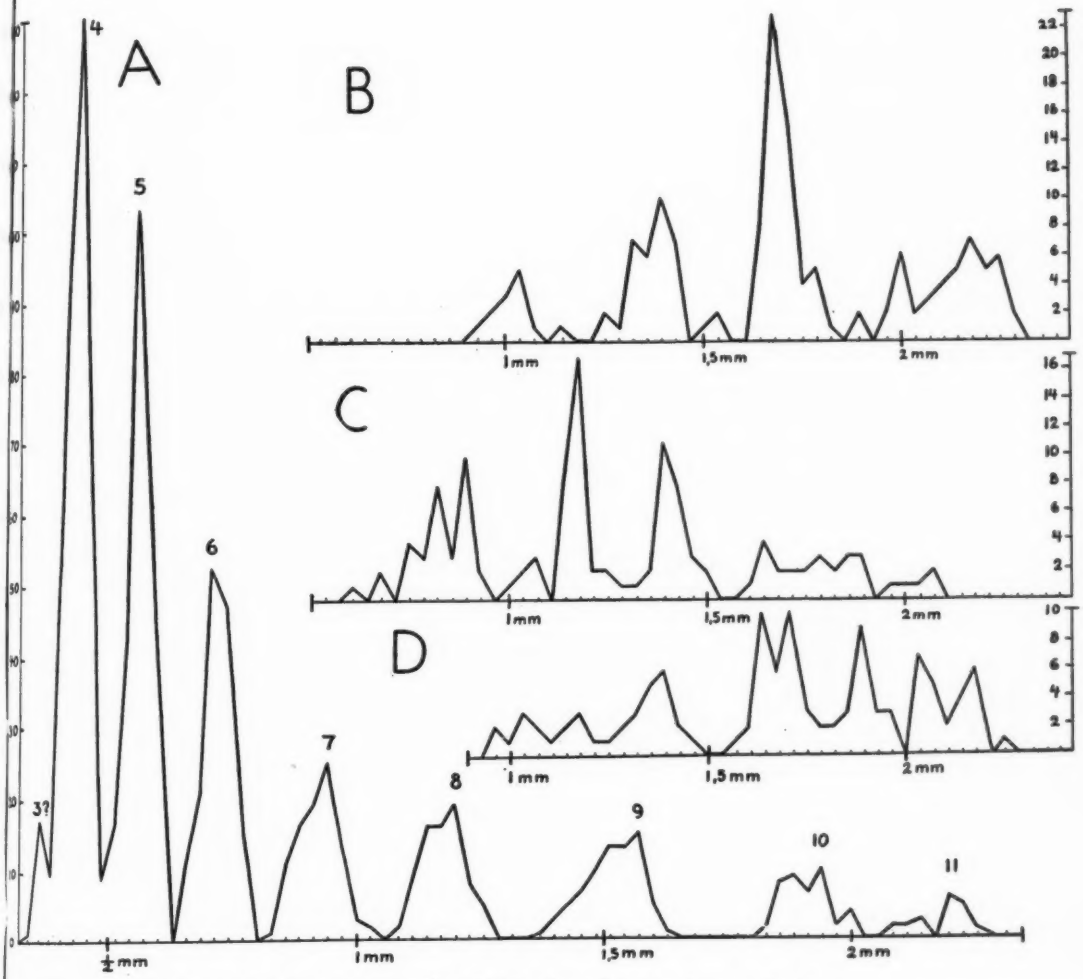


FIG. 2—Graphs showing size and frequency distribution of ostracode growth stages.
A—*Beyrichia jonesi* from the Mulde Tegelbruk, Gotland (Mulde marl, uppermost Wenlock). 972 valves measured.
B—*Beyrichia spinigera* from the upper Visby marl (uppermost Llandovery of lowest Wenlock), Snäckgärdet, Visby, Gotland. 152 valves measured.
C—*Beyrichia jonesi* from the same locality. 122 valves measured.
D—*Beyrichia jonesi* from the Slite group (middle Wenlock), Kvarnberget, Slite, Gotland. 114 valves measured.

mens are known only from cross-sections in brood pouches it is difficult to trace the development of the sulci. The valves have an outline quite like that at later stages. They are 0.003 mm. thick and are covered with long, thin spines, up to 0.012 mm. in length, especially along the margin. Fine perforations occur between the spines.

Stage 3.—(pl. 103, fig. 2.) The mean length is 0.34 mm. Specimens are known both in brood pouches and free and one may assume that the young became free-living at this stage. The valves are 0.007 mm. thick and covered with blunt spines, relatively much shorter than in stage 2 (0.015 mm. long and 0.010 mm. in diameter). The valves are perforated between the spines as in the preceding stage. The median sulcus (SII) is the only one clearly developed at this stage and only in it is the valve not covered with spines. A row of closely placed thin spines forms a velum along the border. The outline of the valves is somewhat similar to certain species of *Concoecia.*

Stage 4.—(pl. 103, fig. 3.) The mean length is 0.44 mm. The form is like that of stage 3 but a faint carina is developed along the margin. A second sulcus (SIII) becomes apparent.

Stage 5.—(pl. 103, fig. 4.) The mean length is 0.57 mm. The form is like the preceding stage but the carina is stronger and the median lobe (LII) appers.

Stage 6.—(pl. 103, fig. 5.) The mean length is 0.73 mm. Valves are like those of the preceding stage but the carina is stronger especially at the anterior end, the median lobe is more pronounced and the velum somewhat reduced.

Stage 7.—(pl. 103, fig. 6.) The mean length is 0.93 mm. The sculpture is less pronounced on the median lobe, the rostrum is reduced, the carina is stronger, but otherwise specimens are like those of stage 6.

Stage 8.—(pl. 103, fig. 7.) The mean length is 1.19 mm. Sculpture is less prominent all over the valves than in the last stage, the lobes are more pronounced, and radiating ribs occur on the carina.

Stage 9.—(pl. 103, fig. 8.) The mean length is 1.52 mm. This stage is like the preceding one but the ribs are stronger on the carina, and the velum has almost disappeared from the posterior part of the valves.

Stage 10.—(pl. 103, fig. 9.) The mean length is 1.91 mm. The lobes are smoother and the carina stronger than in the last stage.

Stage 11.—(pl. 103, figs. 10–11.) The mean length is 2.17 mm. This is the adult stage and two forms occur, apparently males and females. The brood pouches of the females are spherical swellings of the lowest part of the posterior lobe (LIII), about 0.82 mm. in diameter. The carina extends onto the brood pouch, but the velum passes below and behind its lower part (pl. 104, figs. 1–2).

The males differ only slightly from specimens of stage 10, except in size, and in their relatively greater width. Both sexes are ornamented quite differently from the young. They bear scattered pustules containing numerous bulb-shaped bodies with central pores all filled with dark brown matrix (pl. 104, figs. 5–6). The pustules occur on the protruding parts of the median and posterior lobes (LII and III) and on the females also in the furrow above the brood pouch (pl. 104, fig. 5).

Conclusions.—1) There are at least ten, and probably 11, growth stages in the ontogeny of *Beyrichia jonesi.* 2) Increase in size at all moultings, except the last, is strictly in accordance with Brooke's law.

NATURE OF POPULATION

Table 1 and the graph in text-figure 2A show that the number of specimens decreases from the earliest entirely free stage to the last. The difference in number from stage to stage is indicated under the heading "loss" in table 1. This represents the sum of the mortality and the net emigration (i.e., emigration less immigration). I have tried to correlate this figure with the number of complete specimens (two valves jointed in natural position) in each stage.

Table 1 suggests that the complete specimens do not represent dead individuals only, because there are more complete specimens (of two valves) than loss in one moulting (4:5). Migration of individuals into or out of this population seems to be unimportant and probably is not responsible for this excess. I am inclined, therefore, to believe that the complete specimens are empty moults, as was supposed by Störmer (1934,

pp. 56–57) for trilobites and merostomes. If dead animals had been present, decomposition and attack by scavengers would probably have resulted in a separation of the valves.

All complete specimens, both young and adult, are filled with clear calcite although they are embedded in marl. This indicates that the empty valves closed immediately after moulting and suggests the presence of ligaments for closing the valves, not opening them, as in most recent forms (cf. Sohn, 1949).

The Mulde population of *Beyrichia jonesi* seems to have been extremely stable and completely preserved. The other populations are, however, as shown in table 2 and text-figures 2B to D, not so completely preserved. In the Visby population (text-fig. 2C) some specimens with brood pouches are comparable in size to individuals of stage 10. This might be interpreted as an early development of sexual dimorphism. On the other hand, it seems more probable that the smaller mature specimens are adults of another population which inhabited a different and perhaps warmer environment. In some recent ostracode and copepod species individuals living in warmer water develop more rapidly and are smaller at maturity than those living in colder water.

ORIENTATION

The orientation of the fossil ostracodes has been much discussed. That most commonly accepted (Bonnema, 1931, etc.; Triebel, 1941; Hessland, 1949; Levinson, 1950) is based chiefly upon careful studies of modern species, as follows: 1) The median sulcus is directed postdorsally. 2) The adductor muscle impression, located in the lower part of the median sulcus, is central or anterior. The latter, however, is not always valid for the young stages.

In two living suborders, Platycopa and Podocopa, the young hatch as nauplii provided with first and second antennae, mandibles and maxillae. The adductor muscle impression, usually located above the maxillae, is situated posteriorly in the early stages, and migrates forward as the other appendages are added (generally one pair at each moulting in living forms). The muscle impression has a posterior position through the first five stages, and moves to the middle or becomes anterior in the later stages because the posterior part develops considerably faster than the rest of the body (allometric growth) (cf. table 4). The orientation of specimens belonging to the Platycopa or Podocopa, therefore, can not be determined by the position of the adductor muscle impression unless one is positive that the specimens belong to a stage older than stage 5. This is unfortunate, because most of the smooth-valved Paleozoic ostracodes probably belong to these groups.

The ontogeny of the suborder Cladocopa is unknown.

In the Myodocopa the young are hatched with all appendages developed and the posterior part of the body grows only slightly faster than the anterior part. It might be assumed, therefore, that the adductor muscle occupied a nearly central or slightly anterior position during all stages of development.

The criteria mentioned above suggest that the brood pouches of the beyrichids are anterior. A reverse orientation has, however, been accepted by some paleontologists (Ulrich and Bassler, 1923; Kummerow, 1924, 1931, etc.), whose chief argument is that the brood chambers of practically all Recent ostracodes are posterior. In some fossil ostracodes (e.g., Eurychilinidae), however, structures interpreted as brood chambers are located anteriorly (Triebel, 1941).

Characters of *Beyrichia jonesi* and related species which may or may not furnish evidence regarding orientation are as follows:

1) The median sulcus (SII) of *B. jonesi* is not significant as it is triangular in shape, nearly vertical and somewhat indistinct because of the overhanging median lobe (LII).

2) The median sulcus (SII) of *Beyrichia jonesi* is nearly central in position (table 4) and therefore not useful for orientation. If growth had been allometric, as in the Platycopa and Podocopa, this would have been evident in the complete series of growth stages.

In most of the beyrichids this sulcus is so situated. In *Beyrichia maccoyana sulcata* Reuter, *B. tuberculata gibbosa* Reuter (1885, pl. 26), *B. steusloffi* Krause and *Dibolbina cristata* Ulrich & Bassler (1923, pl. 63, fig. 15), however, it may be anterior because it is

nearer the end opposite to that which carries the pouches. These relations are not certain and in *Craspedobolbina dietrichi* Kummerow the median sulcus is probably posterior.

Major spines and significant hinge structures are lacking in *B. jonesi*.

The brood pouches of females of *B. jonesi* may mark the posterior. This is consistent with the gradual "filling out" posteriorly during the ontogenic development (cf. Kellet, in Levinson 1950) observed in this species. Also the occurrence of a rostrum and

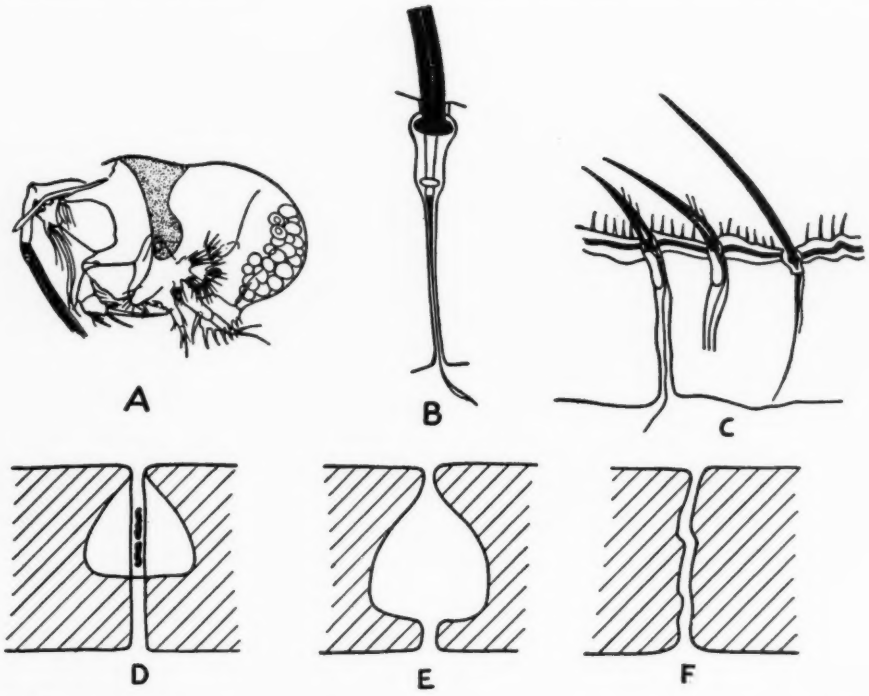


FIG. *3*—Valve structures.

A—The body of *Concoecia magna* (female) showing by shading the area of attachment to the valve (from Müller, 1926, fig. 349). B—Hairbase of *Bairdia serrata*, 1000× (from Müller, 1894, pl. 37, fig. 4). C—Hair bases of *Bairdia* sp., 400× (from Müller, 1894, pl. 36, fig. 60). D—Diagrammatic section through a bulb-shaped pore of *Beyrichia jonesi*, 600×. E—Bulb-shaped pore of *Macronotella fabuliformis*, 600× (redrawn from Hessland, 1949, pl. 12, fig. 5). F—A simple pore, 600×.

In figures B to F the outside is up.

EXPLANATION OF PLATE 103

Growth stages of *Beyrichia jonesi* Boll of the Mulde marl from Mulde Tegelbruk, Gotland. Unretouched photographs.

FIG. *1*—Thin section of an adult female, showing cross-sections of young stages 1 (left) and 2 (right), about ×50.

2—Thin section of an adult female showing cross-section of stage 3, ×30.

3—Stage 4, left valve, ×30.

4—Stage 5, left valve, ×30.

5—Stage 6, left valve, ×30

6—Stage 7, left valve, ×30

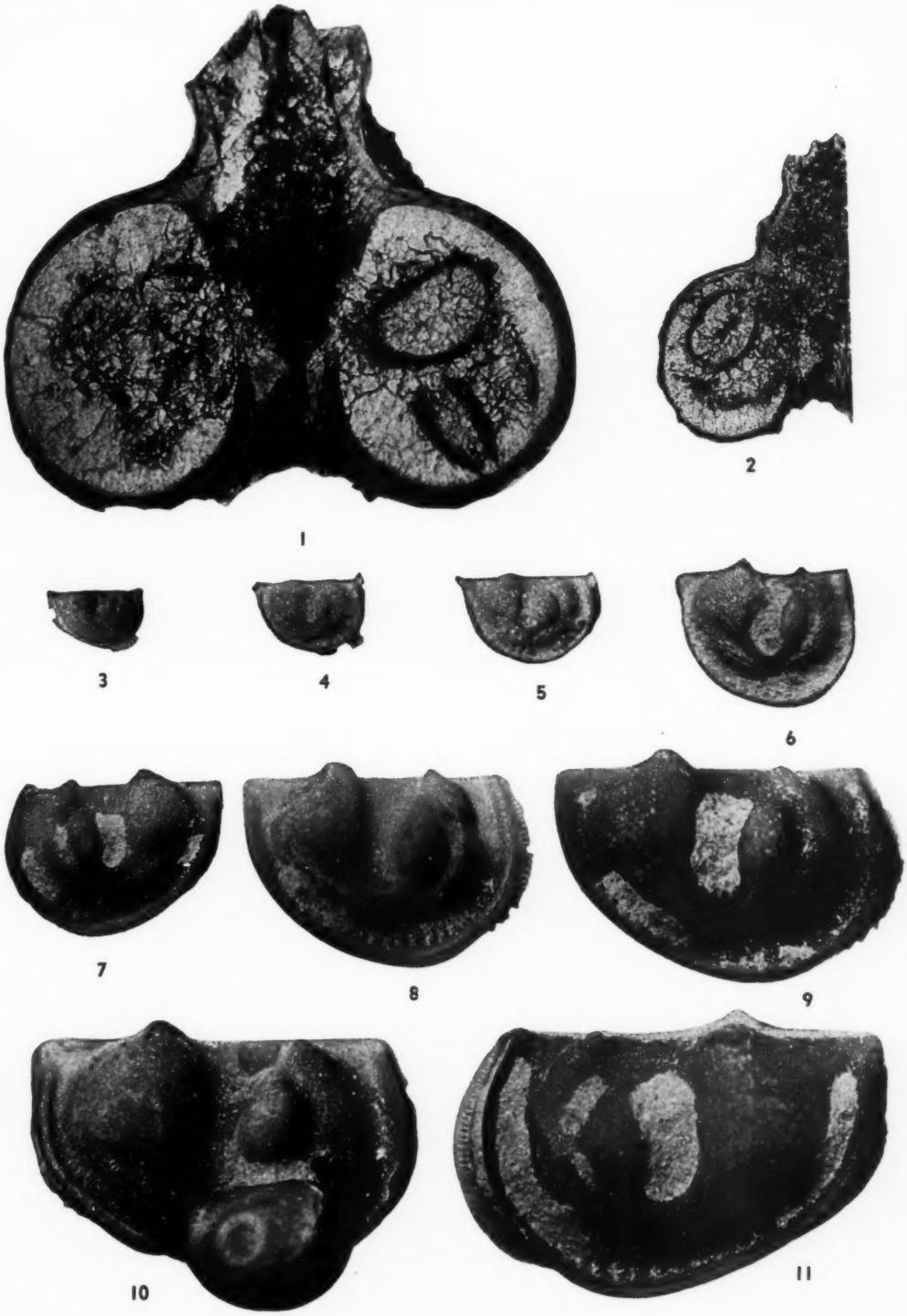
7—Stage 8, left valve, ×30.

8—Stage 9, left valve, ×30.

9—Stage 10, left valve, ×30.

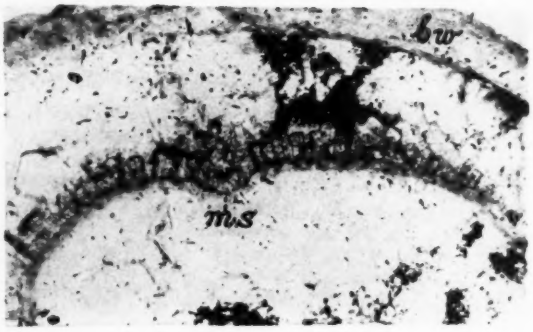
10—Stage 11, adult female, left valve, ×30.

11—Stage 11, adult male, complete specimen showing the right valve, ×30.



Spjeldnaes, *Beyrichia jonesi*

1



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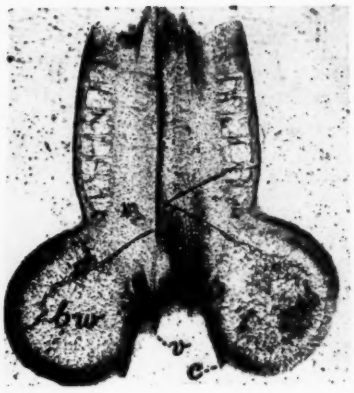

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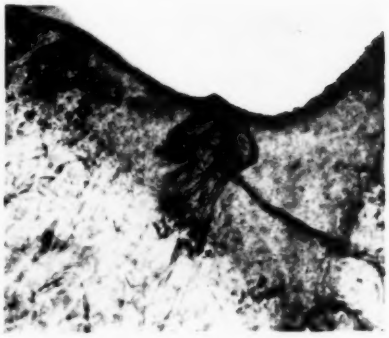
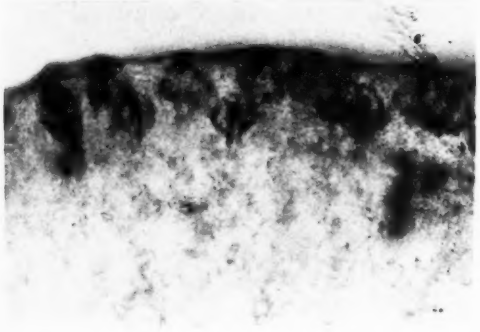
4



5



6

Spjeldnaes, *Beyrichia jonesi*

the *Concoecia*-like general outline of the young (pl. 103, figs. 3–5) is similarly suggestive.

On the whole, a posterior orientation of the brood pouch in the beyrichids seems somewhat more probable.

ORNAMENTATION

Sculpture of the valves of *Beyrichia jonesi* varied considerably during development and two different types of pores occur. Similar pores are known in the Lower Ordovician ostracodes described by Hessland (1949), simple ones (text-fig. 3F) as in *Pinnatulites procera* (Kummerow) and bulb-shaped ones as in *Macronotella fabuliformis* Hessland. The latter differ from those of *B. jonesi*, however, in having no central tube penetrating the bulb (text-figs. 3D to E).

These pores evidently are perforations that were associated either with glands of different sorts or with sense organs such as hairs as in modern ostracodes, but their exact functions in *B. jonesi* cannot be determined. The bulb-shaped perforations resemble hair bases described by Müller (1894) and others in Recent forms (text-figs. 3B to C), but the latter, like the Ordovician species, also seem to lack the central tube.

As pore-like perforations might have been made by boring organisms (cf. Störmer, 1931), several specimens, especially from the Mulde fauna, were sectioned to see if similar perforations occur in other species. They do not. Also the pores are much more regular than the perforations described by Störmer.

No pores or spines occur in the median sulcus, either in adult or in young specimens. Evidently this is because the adductor muscle was attached to the inside of the valves at the bottom of this sulcus, and perhaps the whole median sulcus represents the area where the animal was attached to the valves (text-fig. 3A).

No bulb-shaped pores have been observed in the geologically oldest population of *B. jonesi* from Bisby. Only simple pores occur in both young and adults. Possibly the bulb-shaped pores of the geologically younger adult Mulde specimens, which are preserved in the same manner as those from Visby, are newly acquired characters.

Several other species of *Beyrichia* were also sectioned. If the preservation permits the recognition of their pores, they all appear to be simple, cylindrical ones. Such pores have been found in *B. scanicus* Kolmodin, *B. spinigera* Boll, *B. lindströmi* Kiesow, *B. steusloffi* Krause and *B. klödeni* em. Jones 1888 (not M'Coy).

Perforations of other types also occur in the valves of *B. jonesi*. Along the margin there is a narrow rim, composed of densely placed, probably hollow, spines. Because of similiarities in microstructure and position, these seem to be homologous with the marginal rim (velum) of the Eurychilinidae (= Primitiidae). In the adults the spines are relatively short, and more strongly developed posteriorly. In young specimens the rim is equally developed all around the margin. Studies of thin sections in polarized light show that the spines consist of long calcite fibres oriented with their *c*-axes parallel to the direction of elongation of the spines.

Above the rim is a marginal keel, or

EXPLANATION OF PLATE 104

Microstructure of *Beyrichia jonesi* Boll. The specimens in figures *1–3* and *5*, *6* are from the Mulde marl from Mulde Tegelbruk, Gotland. The specimen in figure *4* is from the upper Visby marl, from Snäckgärdet, Visby, Gotland.

Abbreviations: bw = brood pouch wall, c = carina, ms = median sulcus, r = radiating ribs of carina and v = velum.

FIG. *1*—Section through posterior part of an adult female, showing velum, carina and brood pouch, ×150.

2—Longitudinal section through ventral part of an adult female, showing carina with radiating ribs, velum and brood pouch, ×30.

3—Section through young valve of stage 3. Same specimen as in pl. 103, fig. *2*, ×200.

4—Section through part of anterior lobe (LI) of adult male, showing simple pores. ×200.

5—Longitudinal section of an adult female showing bulb-shaped pores in the furrow adjacent to brood pouch (on right), ×200.

6—Bulb-shaped pores in the anterior lobe (LI) of an adult female, ×150.

carina, bearing radiating ribs (pl. 103, figs. 7–9, 11) which extends onto the brood pouch (pl. 104, figs. 1, 2). The ribs consist of relatively large crystals, which are oriented with their *c*-axes parallel with the ribs. Usually a rib consists of a single crystal but occasionally two or three may occur, and in that case the crystals are usually twinned. Below each rib a comparatively wide, simple pore penetrates the valve.

The velum seems to have been gradually reduced during ontogenetic development, and replaced by the carina, which is probably homologous. In the carina the pores below the radiating ribs are directed outwards, perpendicular to the plane of symmetry, but in the velum they are directed inwards from the margin, in the plane of symmetry. The carinae seem to have finer and more numerous ribs in geologically younger, related species, such as *B. maccoyi* and *B. steusloffi*, which may suggest a repeated development of the velum. In these species the velum-like carina extends onto the brood pouch just as the carina extends onto the brood pouch in *B. jonesi*.

The pores in the velum and in the carina of *B. jonesi* probably correspond to the openings of marginal glands known in recent ostracodes, even though the pores are much more strongly developed in the fossil species. It seems safe to assume that similar pores also occurred in other species of *Beyrichia*, even if they have not been preserved. Such pores have been observed in the carina of *B. maccoyi* and in the velum of *B. steusloffi*. Other species of *Beyrichia*, such as *B. spinigera* and *B. lindströmi* have marginal pores of another type. These, after piercing the valves, continue through long marginal spines.

On the whole, the ornamentation of the beyrichids seems to have been more intimately related to the internal anatomy of the animal than in many Recent ostracodes. If this is true, there may be reason to believe that these characters were less subject to ecological variations and ornamentation and may be of more than ordinary taxonomic value.

TAXONOMY AND PHYLOGENY

The synonomy of *Beyrichia jonesi* is not considered here in detail. The species was founded by Boll in 1856 upon a young valve which, judging by its size, probably belonged to stage 6 or 7. *Beyrichia clavata* Kolmodin 1869, founded on an adult specimen, is a synonym.

Table 4 shows in percentages how much of the valves of two species of *Cypris* (suborder Podocopa) lies anterior to the adductor muscle impression at different stages of development. It also shows in the same way the relative position of the lower part of the median sulcus of *B. jonesi*. Evidently there is a fundamental difference in the larval development of these forms. Growth in *Cypris* is distinctly allometric, but it was isometric in *B. jonesi*.

TABLE 4

Species (from Claus 1872)	Stage	Ant. part. per cent	*Beyrichia jonesi*	
			Stage	Ant. part. per cent
Cypris fasciculata	9	42.5	11	50
	7	44	11	47
	6	47	10	47.5
	5	49	9	47.5
	4	58	8	50
	3	58	7	50
	2	65	6	46.5
Cypris ovum	5	50	5	46.5
	2	64	4	45
	1	69	(3	45–50)

The ontogenetic development of *B. jonesi* resembles that of members of the suborder Myodocopa if the assumption is true that the adductor muscle was attached in the lower part of the median sulcus. Therefore *B. jonesi* and the other beyrichids probably are more closely related to the Myodocopa than to any other groups of modern ostracodes.

The development of *B. jonesi* is not entirely like that of the Myodocopa. Living species of that group have five to seven growth stages, the Podocopa has about nine, and *B. jonesi* 11. Among modern ostracodes, species which hatch at a comparatively advanced stage of development have fewer moults, but the number of stages differs, even within the same genus (Elofson, 1941).

The 11 stages noted in *B. jonesi* probably indicate a primitive condition. No other ostracode is known to have moulted so many times.

In the growth of modern ostracodes, there is usually added at each moult either a new pair of appendages, as in the Podocopa and Platycopa, or an additional joint to appendages already developed, as in the Myodocopa. Because of the large number of growth stages in *B. jonesi* the development of its appendages may have been somewhat different.

The presence of a rostrum in the young stages of *B. jonesi* also suggests relationship with the Myodocopa in all members of which it is more or less developed. In modern forms a frontal opening occurs below the rostrum but this has not been found in any stage of *B. jonesi*. This opening accommodated the organs for the locomotion, the second antennae, which are strongly developed in planctonic forms (e.g., *Concoecia*). These antennae may have been less developed in the apparently benthonic beyrichids.

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INTERNAL STRUCTURE OF *CYCLAMMINA CANCELLATA*

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ABSTRACT—The so-called labyrinthic structure consists of three types of alveoles which appear successively in ontogenetic development. This structure and ontogenetic changes in the aperture suggest that *Cyclammina* evolved from *Haplophragmoides*.

INTRODUCTION

THE interior structure of recent specimens of *Cyclammina cancellata* was described by Brady (1879, p. 62) as being a finely arenaceous tubular growth, almost, and often entirely, filling the chamber lumina. In detailed remarks accompanying the generic definition, published in 1884 (p. 351), he referred to the "peculiar labyrinthic condition of the skeleton" which attains its fullest development in *C. cancellata*. Although the interior structure was regarded by Brady to be labyrinthic (1884, pp. 351–352), he recognized that the tubular passages are regularly constructed and do not perforate the thin outer layer of the chamber walls. In the descriptions of most of the subsequently introduced species of *Cyclammina*, with perhaps the exception of *C. uhligi* Schubert 1901, the interior features of the test are either not mentioned at all or conventionally characterized as labyrinthic (*C. complanata* Chapman 1904, *C. bradyi* Cushman 1910, *C. contorta* Pearcey 1914, *C. compressa* Cushman 1917, *C. constrictimargo* Stewart & Stewart 1930, *C. elegans* Cushman and Jarvis 1932, *C. medwayensis* Parr 1935, *C. praecancellata* Voloshinova 1939, *C. caneriverensis* Hussey 1943, etc.). Schubert (1901, p. 22, pl. 1, fig. 27) very carefully investigated the glycerine preparation of the equatorial section of *C. uhligi* and his observations agree with those made by the writer on the initial portion of *C. cancellata*. Maync (1949, p. 536) considered the complex wall structure of *Cyclammina* to be labyrinthic, but rightly criticized the inaccurate use of this term. In the writer's opinion, it should be reserved for the description of wall structures and subdivisions of chambers where no regular arrangement of the structural elements can be seen (Bronnimann, 1951).

C. cancellata occurs abundantly in the clays of the Miocene Cruse and Forest formations of South Trinidad ("*Cyclammina* clays" of earlier authors) and the following notes on the interior structure are based on numerous well-preserved and occasionally ironstained specimens and fragments as well as on some axial and equatorial sections. The figured specimens are deposited in the Cushman collection of the U. S. National Museum, Washington, D. C.

Preliminary investigation of fragments and of sectioned specimens revealed the so-called labyrinthic structure to be confined to the thick outer walls. Oblique equatorial sections which did not touch or only slightly cut the chambers, however, were generally interpreted as if the chamber lumina were obliterated by the peculiar "interior growth" (Brady, 1884, pp. 350, 352, pl. 37, fig. 12). None of the investigated specimens has chambers filled with the interior structure. It also became evident that the wall structure is of a *non-labyrinthic alveolar nature* [=tubular passages (Brady), Kanäle (Schubert)], undivided in early ontogenetic stages but branching in the last chambers. Three types of alveoles (here designated, primary, secondary, and tertiary) are arranged in a definite and regular pattern, and can be distinguished in successive ontogenetic stages.

PRIMARY ALVEOLES

This most primitive type of alveole is developed at different ontogenetic stages of the two generations which therefore are separately treated.

Megalospheric individuals.—Equatorial sections of the initial portion of megalo-

spheric specimens (figs. 1, 2) show plain elongate and undivided alveoles, here termed primary alveoles, which do not perforate the thin epidermal layer. These primary alveoles are arranged normal to the outer walls of the chambers. Alveoles are absent in the slightly curved septa proper. The chambers are connected by slit-like apertures at the base of the septa (inferiomarginal aperture) as in *Haplophragmoides* Cushman 1910 emend. Höglund 1947. Small subcircular openings on the inner wall of the initial chambers indicate that primary alveolar cavities are already present at this very early ontogenetic stage. Sections demonstrate that the alveolar openings toward the chamber lumina are distinctly constricted and that occasionally the alveoles narrow to form tubular canals (figs. 1, 2, 4–6). The alveoles increase in number with the size of the chambers. Alveoles of the initial chambers are of the same type but smaller than those of the adjacent early ontogenetic spiral stage. The outer walls carrying the alveolar cavities are much thicker than the septa, in places twice as thick. The chamber cavities are not obliterated by the alveolar structure.

Microspheric individuals.—Primary alveoles appear in the outer chamber walls of microspheric individuals (fig. 3) after approximately two whorls (15th to 16th spiral chamber). The alveoles are of the same primitive type but much larger than in the megalospheric specimens, and their openings are more tube-like. The early alveoles are conspicuously large and it is not impossible that they belong to an ontogenetic stage not existing in megalospheric individuals. The alveoles of the megalospheric initial chamber seem to be related to this type of primary alveole (figs. 4, 5, 6). No alveoles have been recognized in the wall of the initial chamber or in the septa proper. The chambers of the early ontogenetic stage communicate by slit-like basal apertures. Only a very few good sections were available and it should be stressed that the features of the initial portion of microspheric individuals need further investigation.

SECONDARY ALVEOLES

Secondary alveoles are small peripheral outgrowths of the large primary cavities with which they communicate by narrow, often tubular passages (figs. 4, 6). This type of alveole occurs in the ontogenetic stages of both generations immediately following that characterized by the primary alveoles. No differences between the two generations have been noticed as far as the first appearance and the development of the secondary alveoles are concerned. In sections, usually one to three secondary alveoles branch from one of the large primary alveoles, and broken portions of the outer wall clearly show that the secondary alveoles grow in various peripheral directions but always normal to the outer wall. This arrangement of primary and secondary alveoles is dendroidal. The first indication of the development of secondary alveoles invariably is to be found in the equatorial plane where the outer chamber wall attains its greatest thickness. Axial sections (figs. 4, 5) show that the alveoles close to the spiral axis are still of the primary type, whereas those in the equatorial plane are already composite, consisting of primary alveoles with dendroid outgrowth of secondary alveoles.

TERTIARY ALVEOLES

Tertiary alveoles are minute peripheral dendroid outgrowths of the larger secondary cavities (figs. 7, 8, 13). Connection and arrangement is fundamentally the same as that described for the secondary alveoles. Ontogenetically they appear after the full development of the secondary alveoles and no differences between the two generations have been recognized in this respect. The first tertiary alveoles occur in the equatorial plane of the test where the outer wall reaches its maximum thickness (fig. 8). Typical occurrences of the full dendroidal development of the alveolar system, can be observed in the last ontogenetic stages of *C. cancellata* (figs. 7 and 13). Figure 13 represents the interior portion of the broken end chamber of a large adult specimen. The section through the alveolar system on the right hand side lies in the equatorial plane and displays clearly the three peripherally directed types of alveoles. The section below cuts almost perpendicularly to the outer wall and parallel to the septum. Larger openings to the dendroidal system of sec-

TABLE 1

Megalospheric generation	*Microspheric generation*
a) Not present	a) Spiral of about two whorls without alveoles.
b) Stage with primary alveoles. It is possible that the microspheric generation exhibits a more primitive stage with very large primary alveoles not present in the megalospheric individuals.	
c) Stage with primary and secondary alveoles.	
d) Stage with primary, secondary and tertiary alveoles.	

ondary alveoles and some smaller openings to the tertiary alveoles are visible in both sections.

The eroded surfaces of specimens of *C cancellata* exhibit a complex pattern of small pits of various sizes which can only be correctly interpreted after the analysis of the alveolar system as a whole. The adult specimen reproduced in figure 12 (probably a microspheric individual) has been eroded superficially, at least near the periphery. The numerous minute subcircular openings along the margin of the eroded portion are cross-sections of the tertiary alveoles. In an inner area appear the less numerous, but larger sections of the secondary ones and finally in the central portion of the cut area the large sections of a few primary alveoles. Near the umbilicus secondary and few tertiary alveoles again are evident. The specimen of figure 11 has been cut deeper, thus disclosing besides some secondary ones mostly primary and virtually no tertiary alveoles. Eroded surfaces of ontogenetically younger stages with only primary and secondary alveoles are represented by figures 9 and 10.

The minute tertiary alveoles are occasionally visible in specimens with a glass-like, transparent surface (individuals with recrystallized or chemically changed test as found in older or tectonically stressed deposits). The tertiary alveoles appear to be arranged in small independent groups which correspond to the dendroidal system branching from an individual primary alveole.

ONTOGENY AND PHYLOGENY

Based on the development of the alveolar system, the ontogeny of *C. cancellata* is differentiated into the stages shown in table 1.

It is of interest to note that the microspheric individuals possess a short spiral without alveoles preceding the ontogenetic

EXPLANATION OF FIGURES

FIGS. *1–12*—*Cyclammina cancellata*, Lower Miocene, South Trinidad. *9*, *10* and *12*, ×29.5; all others, ×68.5. Structures identified: (1) primary alveoles, (2) secondary alveoles, (3) tertiary alveoles, (4) openings of primary alveoles, (5) openings of secondary alveoles, (6) openings of tertiary alveoles, (7) initial chamber, (8) spiral chamber, (9) equatorial plane where shell is thickest.

1, *2*—Sh. 1158; T.L.L. Cat. No. 158509. Equatorial sections of megalospheric individuals showing primary alveoles in the outer walls (finely stippled) and openings of alveoles into the initial chamber and the spiral chambers (white stippled). Apertures are basal slit-like openings.

3—Sh. 1429–1459; T.L.L. Cat. Nos. 159331–159343, 159347–159361. Equatorial section of microspheric individual with non-alveolar early spiral. The adjacent portion of the spiral with primary alveoles in the outer walls (finely stippled) and openings of alveoles into the spiral chambers (white stippled). Apertures are basal slit-like openings.

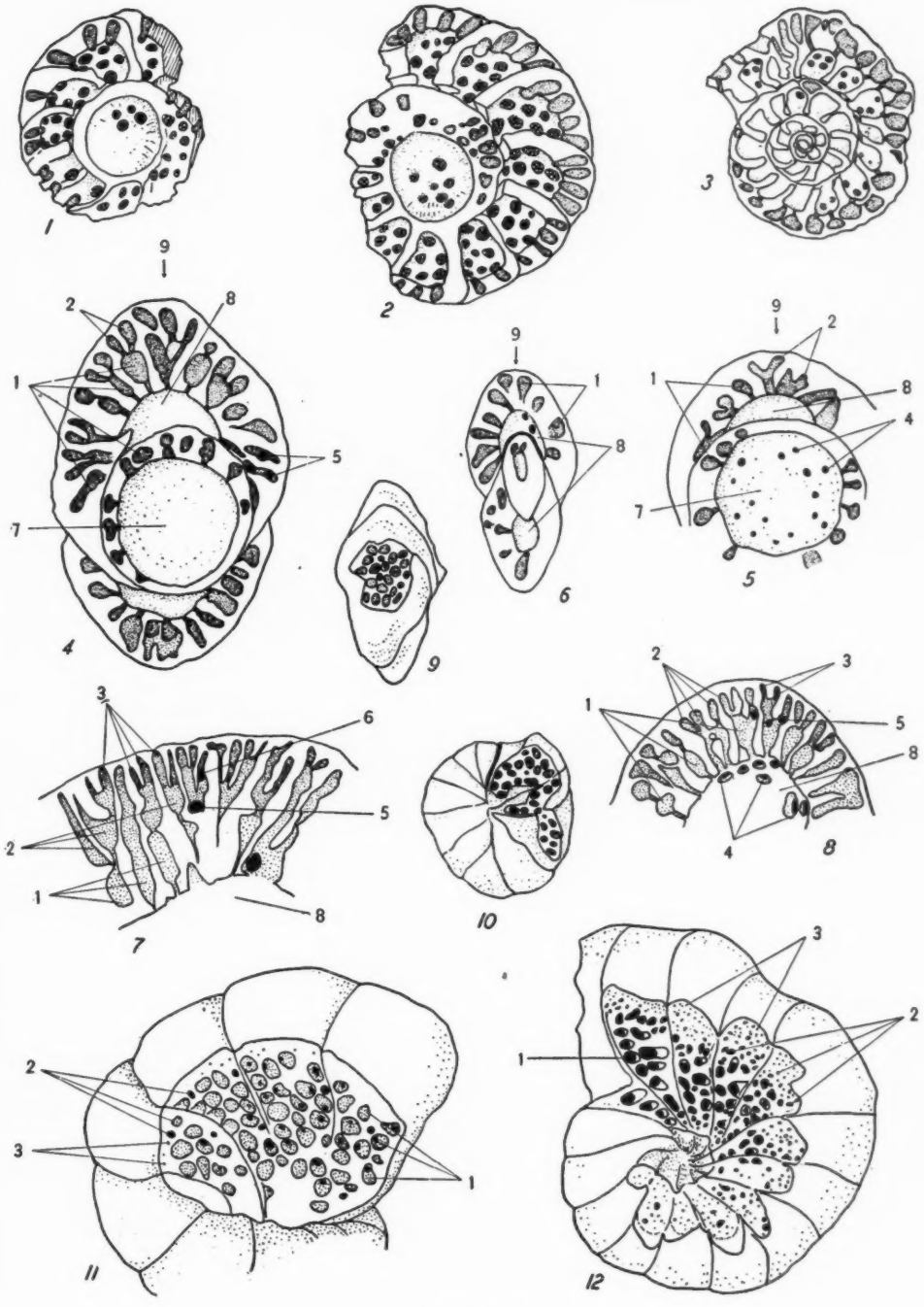
4–6,—*4*, *5*, private collection, axial sections of megalospheric individuals. *6*, Sh. 1429–1459; T.L.L. Cat. Nos. 159331–159343, 159347–159361. Axial section of possibly microspheric individual showing primary and secondary alveoles, initial and spiral chambers, openings into primary and secondary alveoles.

7, *8*—*7*, Sh. 1429–1459; T.L.L. Cat. Nos. 159331–159343, 159347–159361. *8*, Sh. 1477; T.L.L. Cat. No. 160067. Portions of axial sections showing primary, secondary and tertiery alveoles and openings of alveoles into chamber.

9, *10*—*9*, Sh. 1417; T.L.L. Cat. No. 159319; *10*, Sh. 1418, T.L.L. Cat. No. 159320. Young specimens with eroded surface showing primary and (?)secondary alveoles and basal slit-like aperture.

11—Sh. 2008; T.L.L. Cat. No. 160578. Specimen with strongly eroded surface. showing primary, secondary and tertiary alveoles.

12—Sh. 1867; T.L.L. Cat. No. 160542. Adult specimen with only slightly eroded surface showing clearly the areal distribution of the three types of alveoles.



FIGS. 1–12

stages characterized by the alveolar systems. This non-alveolar portion of the spiral is not present in the ontogenetically more advanced megalospheric generation.

Other features of *C. cancellata*, for instance, the shape of the aperture, evolve in parallel ontogenetic series similar to the one described above. The most primitive type of aperture is a basal slit-like opening identical with that of *Haplophragmoides* Cushman emend. Höglund. The slit-like opening becomes more and more reduced and the last chambers communicate through a composite aperture consisting of an almost closed basal slit and a number of large pores distributed over the apertural face.

The probable ancestor of *Cyclammina* therefore appears to be a form without alveolar system and with an inferio-marginal aperture, related to *Haplophragmoides*. *Alveolophragmium* Stschedrina 1936 (genotype: *A. orbiculatum* Stschedrina 1936, Recent, Japan Sea), with small cavities like primary alveoles in the outer walls (Wabenschicht), cannot represent the ancestral form of *Cyclammina*, as demonstrated by the primitive features of the microspheric generation. Phylogenetically, both *Cyclammina* and *Alveolophragmium* must be interpreted as higher differentiated offshoots from the simply structured, non-alveolar genus *Haplophragmoides* (Cushman, 1948,

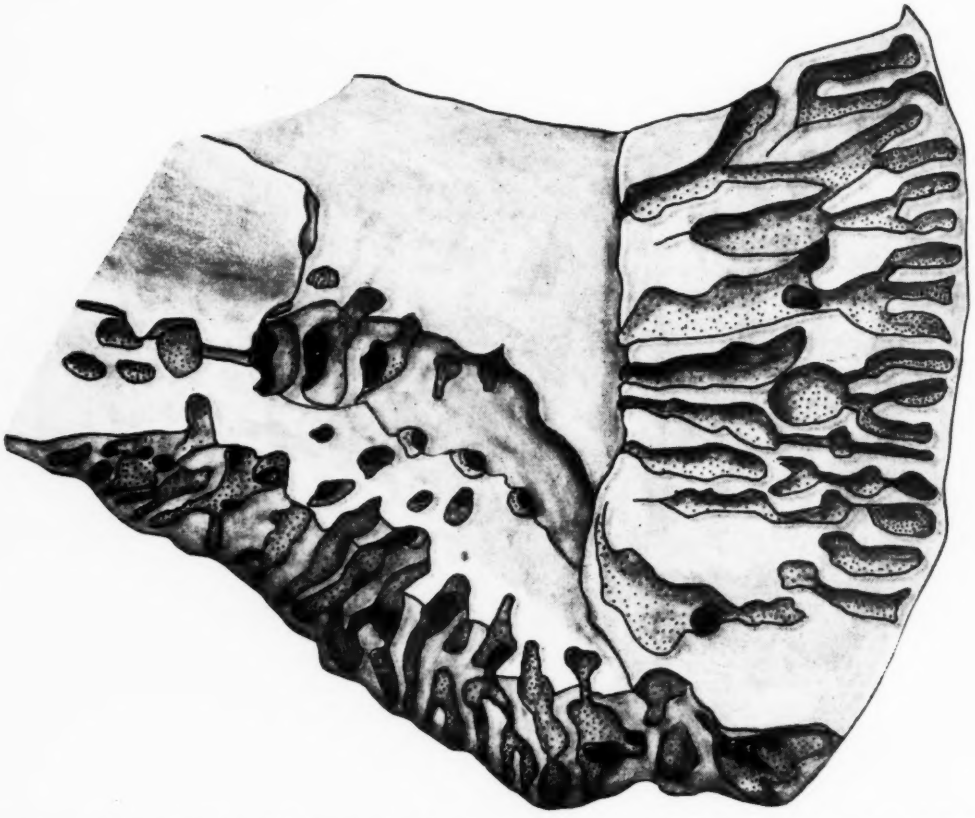


FIG. *13*—Diagram of internal structure of last ontogenetic stage of *Cyclammina cancellata*, ×125. Sh. 1429–1459; T.L.L. Cat. Nos. 159331–159343, 159347–159361. Lower Miocene, south Trinidad. Interior of adult chamber with sections through outer walls. Section to right is in equatorial plane, section below is in axial plane; both show the fully developed dendroidal alveolar system. Black areas are openings into alveoles. The slightly curved smooth plate to left originates at contact zone between this chamber and surface of precedent whorl. No details are shown in upper central part of diagram which cuts across septum between curved plate and equatorial alveolar system.

p. 100). Maync (1949, p. 537) however, suggested that "*Cyclammina* has evolved as an aberrant (phylogerontic?) form from *Pseudocyclammina—Lituola*, starting for some reason or another an exuberant irregular growth in the interior of its test."

It is to be expected that stratigraphically older species of *Cyclammina*, as *C.* cf. *garcilassoi* Frizzell (Cushman and Renz, 1946, p. 19, pl. 2, fig. 11), known in Trinidad in the Paleocene Chaudiere and Lizard Springs formations and in the lower to middle Eocene Navet formation, possess a more primitive alveolar system (possibly only primary alveoles) than the highly evolved Tertiary to Recent *C. cancellata*. Analysis of the evolution of the alveolar system and other morphologic features will probably lead in the course of time to the establishment of bioseries within the genus *Cyclammina*. Such a study would considerably clarify the rather obscure taxonomy of this important group of Foraminifera.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, PP. 762–764, PL. 105, NOVEMBER 1951

PEMPHIGASPIS, A UNIQUE UPPER CAMBRIAN TRILOBITE

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ABSTRACT—*Pemphigaspis* was originally based upon pygidia with peculiar swollen pleural lobes. *Hallaspis* was based on associated cranidia and is a synonym. A complete description of *Pemphigaspis* is presented, and two species, *P. bullata* Hall from the Dresbach formation of Wisconsin and Minnesota, and *P. inexpectans* Lochman from the Riley formation in Texas are redescribed and refigured.

DURING studies of the faunas of the Dresbach formation in the upper Mississippi Valley and the Riley formation in Texas, a number of specimens of *Pemphigaspis* have been collected that show fully the characters of the genus and two of the species assigned to it. The swollen kidney-shaped pleural lobes of the pygidia, upon which *Pemphigaspis* was based, are so unusual that these pygidia have not been identified previously as parts of a conventional trilobite. The cranidia which are now assigned to *Pemphigaspis bullata* originally were described by Hall as *Amphion? matutina* and subsequently this species became the genotype for *Hallaspis*. The critical specimen, showing a *Pemphigaspis* pygidium attached to a trilobite thorax of eight segments was discovered in the collections of the University of Minnesota by Dr. W. C. Bell, who identified it and suggested this study. Most of the other specimens were collected during the summers while I was employed by the Minnesota Geological Survey in 1947 and by the Bureau of Economic Geology of the University of Texas in 1948. I am pleased to express my sincere thanks to Dr. Bell and Dr. Christina Lochman for their encouragement and criticism during the preparation of this paper.

Pemphigaspis is a moderately rare early Upper Cambrian trilobite which characterizes the upper portion of the *Crepicephalus* zone of the Dresbachian stage in the upper Mississippi Valley and central Texas. In Montana it is associated with a fauna having lower *Crepicephalus* zone affinities (Lochman, personal communication, 1949).

Hall (1863, p. 221) erected the genus and described a new species, *Pemphigaspis bullata*, for "a crustacean somewhat resembling the pygidium of a trilobite." Lochman (1938, p. 84) described a new species, *P. inexpectans*, from the Cap Mountain limestone in Texas, placing it in "Phylum undetermined." In a later paper (Lochman and Duncan, 1944, p. 79) she interpreted a similar Montana form to be chonchostracan, stating,

> The specimen shows very nicely the under surface which ends in an elliptical narrow raised rim,—definitely suggesting that this form was a type of carapace of two equal halves covering the anterior portion of the body similar to that found among the conchostraca.

Following his description of *Pemphigaspis bullata*, Hall (1863, p. 222) described another new species, *Amphion? matutina*, based on a fragmentary cranidium from the same locality. This species has been referred to several different genera by later authors, and was finally made the genotype of *Hallaspis* (Raasch and Lochman, 1943, p. 229).

Evidence now indicates that the cranidia of *Hallaspis* actually are *Pemphigaspis* heads. In Minnesota the heads and tails occur in moderate abundance in a narrow zone where they are associated with few other species. In Texas they are known from one locality in a large and varied fauna. Only two other genera, *Crepicephalus* and *Maryvillia*, are common to these two assemblages. In Montana one specimen each of a head and a tail are recorded from a single locality and zone in the Little Belt Mountains (Lochman and Duncan, 1944, p. 21).

Redescriptions of *Pemphigaspis* and the two species available to me follow. In addition to these species and the one from Montana, Butts (1936, p. 14) has reported *Pemphigaspis* cf. *bullata* from the Warrior

limestone in Pennsylvania, and Resser (1938, p. 92) has described a new species, *P. appalachia*, from the southern Appalachians.

SYSTEMATIC DESCRIPTION

Genus PEMPHIGASPIS Hall, 1863

Pemphigaspis HALL, 1863, New York State Cab. Nat. History, 16th Ann. Rept., p. 221.
Hallaspis RAASCH & LOCHMAN, 1943, Jour. Paleontology, vol. 17, p. 230.

Small opisthoparian trilobites with cranidium subtrapezoidal in outline, median width very slightly greater than length, strongly convex transversely, moderately convex longitudinally, anterior margin nearly straight, anterolateral corners rounded. Glabella relatively large, expanding slightly forward, broadly rounded at front, extending to and slightly overhanging anterior margin, sides short, steep, top gently to moderately convex with a faint median longitudinal ridge, median width about half that of cranidium. Three pairs of glabellar furrows, anterior pair very faint, pitlike, second pair moderately well impressed, posterior pair strongly arcuate, very deeply impressed, especially at inner ends. Occipital furrow broad, deep. Occipital ring with short median spine. Dorsal furrow deep at sides of glabella. Brim narrow, present only in front of fixed cheeks. Border where present, narrow, horizontal, absent on some forms, separated from cranidium by anterior branch of facial suture which appears to be in marginal furrow and tangent to anterior end of glabella. Fixed cheeks triangular, moderately convex, downsloping, narrowest anteriorly. Palpebral lobes very long, narrow, slightly arcuate, front ends close to and opposite anterior third of glabella, diverging posteriorly at nearly 45° from longitudinal axis, posterior ends opposite posterior pair of glabellar furrows. Ocular ridges short, weak. Posterior limbs short, triangular, length about equal to that of occipital ring. Posterior furrow broad, deep. Anterior course of facial suture variable. Posterior course makes angle of about 45° with longitudinal axis.

Free cheek narrow, elongate, margin broadly curved. Border convex, nearly as wide as ocular platform. Marginal furrow deep, broad. Genal spine long, straight, slender, making definite angle with margin of cheek, joining cheek at extreme posterior corner. Anterior continuation of cheek possibly extended to midline of cephalon on some forms.

Thorax subrectangular, moderately convex, consisting of at least eight segments. Axis well defined, dorsal furrows subparallel.

Pygidium subtriangular but swollen bulbous pleural lobes make it appear subovate in dorsal view, width about one and one-half times length. Axis narrow, evenly tapering, well defined, consisting of about four to six well marked segments and a terminal portion. Terminal portion about three times length of last segment, expanding posteriorly to narrow, rimlike border that extends forward on ventral surface. Pleural lobes strongly swollen, kidney-shaped, higher than axis, expanding laterally beyond ventral rimlike border to a maximum distance slightly less than width of axis on small specimens.

Surface of test finely granulated.

Remarks.—This description is based upon the study of numerous cranidia and pygidia of *Pemphigaspis bullata* Hall from several localities along the Mississippi River in Minnesota and a large number of cranidia, three pygidia, and a free cheek of *Pemphigaspis inexpectans* Lochman from one locality in Mason County, Texas. The very long eyes and large, anteriorly expanding glabella are the most striking features of the head of this genus and serve to distinguish it from all other known forms. The pygidium cannot be confused with that of any other trilobite and it is easily identified by its swollen, kidney-shaped pleural lobes.

PEMPHIGASPIS BULLATA Hall
Plate 105, figures 3–6

Pemphigaspis bullata HALL, 1863, New York State Cab. Nat. History, 16th Ann. Rept., p. 221, pl. 5a, figs. 3–5.
Amphion? matutina HALL, 1863, New York State Cab. Nat. History, 16th Ann. Rept., p. 222, pl. 5a, fig. 6; ——, 1867, Albany Inst. Trans., vol. 5, p. 194; WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 219, pl. 26, fig. 8.
Acheilus matutinus, RAYMOND, 1924, Vermont State Geologist Rept., p. 167.
Stenochilina matutina, RESSER, 1936, Smithsonian Misc. Coll., vol. 95, p. 27.
Hallaspis matutina, RAASCH & LOCHMAN, 1943,

Jour. Paleontology, vol. 17, p. 230, pl. 34, figs. 14–17; LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 69, pl. 5, fig. 9.

Pemphigaspis sp. LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 79, pl. 4, fig. 27.

Not *Pemphigaspis* cf. *bullata* BUTTS & MOORE, 1936, U. S. Geol. Survey Bull. 855, p. 14.

Trilobites belonging to *Pemphigaspis* with border of cranidium absent. Anterior course of facial suture intramarginal, tangent to front of glabella. Axis of pygidium tapering gently posteriorly. Axial segments usually five, narrowing slightly towards rear. Terminal portion curved downward and somewhat forward.

Occurrence.—Upper Cambrian, Eau Claire member of the Dresbach formation. Univ. Minn. localities: F6.1P—Millers Corner, 3.2 miles north of Root River crossing of highway 16, outside of Hokah, Minn.; F53.1P—one mile south of La Moille, Minn.; F59.2P—La Crescent, Minn.; U. S. Nat. Mus. locality 86, Dresbach, Minn.

Hypotypes.—University of Minnesota—T6590a, T6590b, T6591.

Remarks.—The cranidia of *P. bullata* and *P. inexpectans* do not seem to be distinguishable but these species can be separated easily by differences of the pygidial axes and their segments. Both differ from *P.* cf. *bullata* Butts & Moore by lacking a border on the cranidium.

PEMPHIGASPIS INEXPECTANS Lochman
Plate 105, figures 7–9

Pemphigaspis inexpectans LOCHMAN, 1938, Jour. Paleontology, vol. 12, p. 84, pl. 17, figs. 27, 28.

Cephalon similar to *P. bullata.* Thorax unknown. Pygidium with axis tapering strongly posteriorly. Axial segments six, narrowing rapidly towards rear. Terminal portion not curved downward.

Occurrence.—Upper Cambrian, Cap Mountain member of the Riley formation: From outcrop in bed of south fork of Morgan Creek, 4.2 miles northwest of highway 29, Burnet County, Texas (Univ. Texas Bur. Econ. Geol. loc. 27T-8-36A); zone 201 in James River section, 1 mile up James River from junction with Llano River, Mason County, Texas.

Holotype.—U.S.N.M. 95016, South Fork of Morgan Creek. Hypotypes: UT-31921–31925.

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EXPLANATION OF PLATE 105

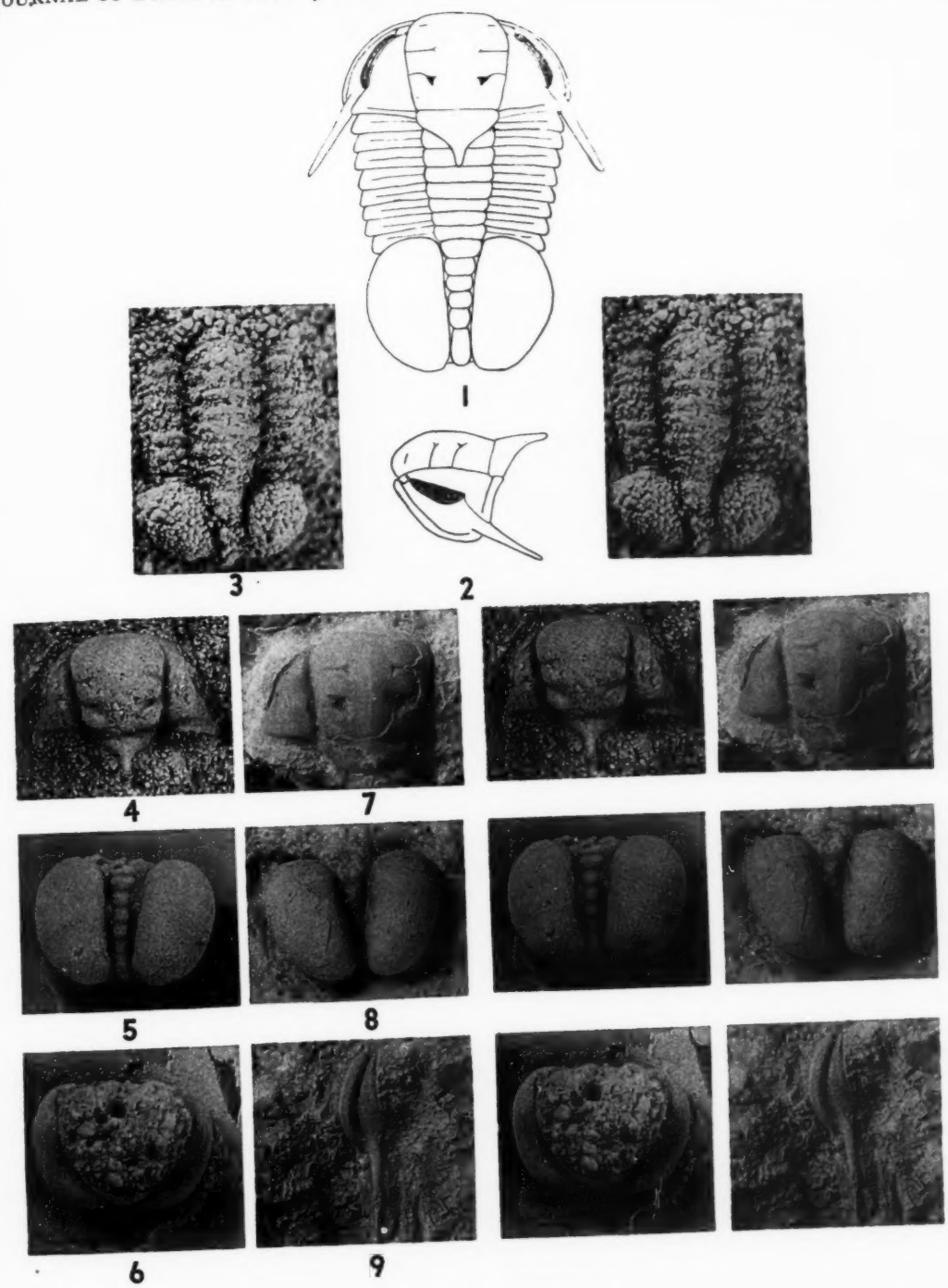
Figures *3–9* are stereoscopic pairs.

FIG. *1*—Reconstructed drawing of dorsal view of *Pemphigaspis* with intramarginal facial suture; about ×5.

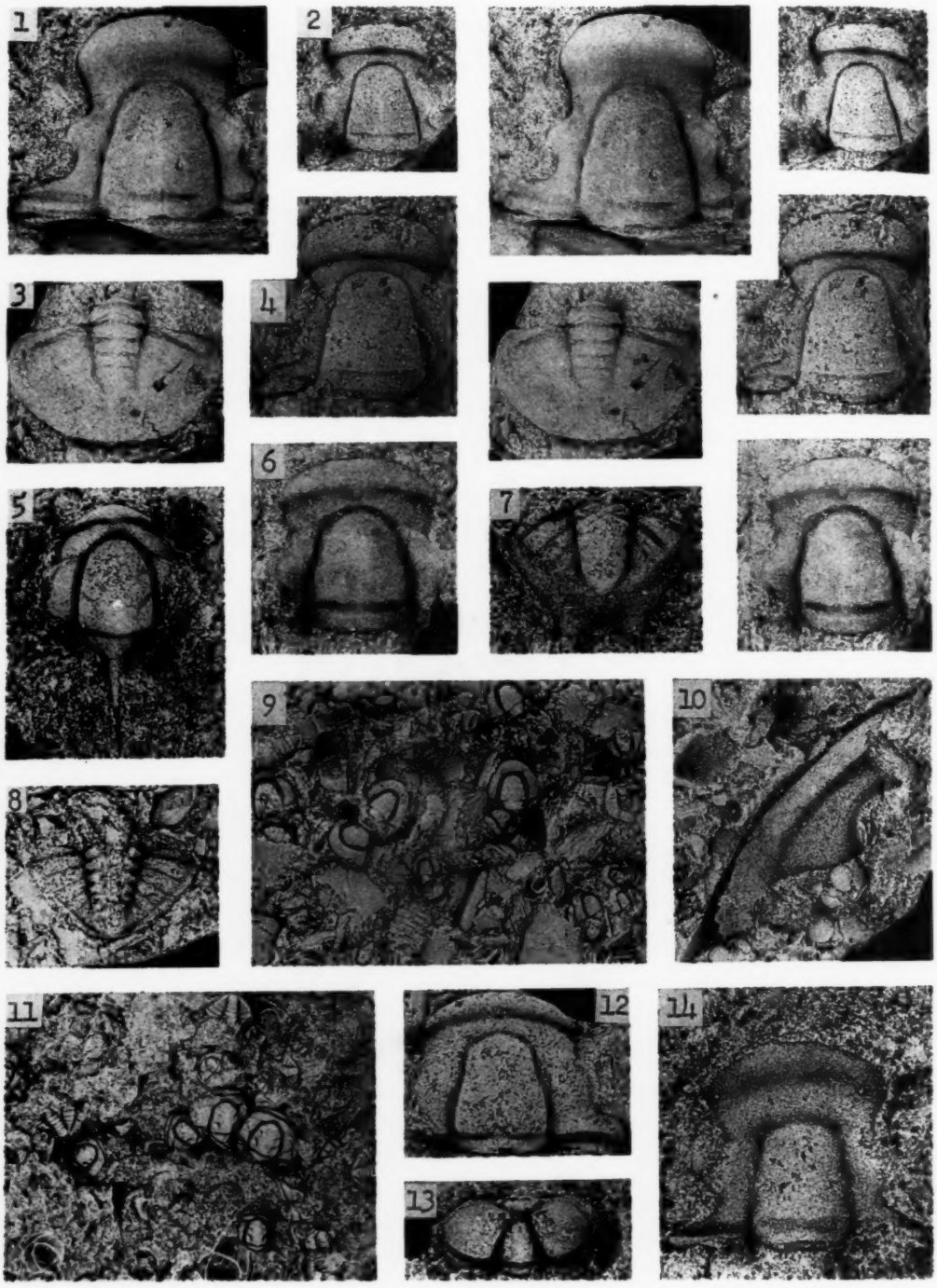
2—Profile drawing of head at same magnification.

3–6—*Pemphigaspis bullata* Hall. *3*, Hypotype; part of thorax and pygidium; ×7; T6590a, La Moille, Minn. This specimen demonstrates that *Pemphigaspis* was a trilobite. *4*, Hypotype; cranidium ×5; T6590b, La Moille, Minn. *5*, *6*, Hypotype; pygidium; ×6; T6591, La Crescent, Minn. Dorsal and ventral views of the same specimen. (p. 763)

7–9—*Pemphigaspis inexpectans* Lochman. *7*, Hypotype; cranidium, ×5; UT-31921, zone 201, James River section, Mason County, Texas. Shows the long palpebral lobes, very faint anterior furrow and median keel, and granular surface. *8*, Hypotype; pygidium; ×5; UT-31922; locality same as figure *7*. Shows the strongly tapering pygidial axis. *9*, Hypotype; free cheek; ×5; UT-31923; from same piece of limestone as specimen in figure *7*. Anterior end broken off. (p. 764)



Palmer, *Pemphigaspis*



Nelson, Cambrian trilobites

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CAMBRIAN TRILOBITES FROM THE ST. CROIX VALLEY

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ABSTRACT—The trilobite faunas of the St. Croix valley in Minnesota and Wisconsin represent the *Crepicephalus* and *Aphelaspis* zones of the Dresbach formation, the *Elvinia*, *Conaspis* and *Ptychaspis-Prosaukia* zones of the Franconia formation, and the *Osceolia* fauna and upper *Dikelocephalus* zone of the St. Lawrence and Jordan formations. Representative forms are illustrated and three new genera and 13 new species and variants are described and figured.

INTRODUCTION

CAMBRIAN strata of the St. Croix valley, which lies along the boundary between Minnesota and Wisconsin, constitute the type section for the North American Upper Cambrian. With the exception of studies by Ulrich and Resser (1930, 1933) on the upper part of the section, little systematic work has been published on the faunas of this area since the early work of Owen, Whitfield, Hall and Walcott. The faunas of the various zones of the Franconia formation have been particularly neglected and few illustrations of their fossils have appeared in the literature during the present century.

The stratigraphy of the St. Croix valley was studied in the field under the auspices of the Minnesota Geological Survey during the summers of 1946, 1947 and 1948, and collections were made at all available sections. The nature of the exposures, the few outcrops of each fossil zone, and the generally poor preservation of the specimens have resulted in a relatively meager fauna compared to collections obtained from similar strata in central and western Wisconsin. All determinable species and variants were studied in detail, and the new genera, species and variants are described and illustrated. Only the best preserved specimens of the most common previously described species are illustrated and discussed.

Acknowledgments are due particularly to Professor W. Charles Bell of the University

EXPLANATION OF PLATE 106

Dresbach formation—Eau Claire member
(Figure *1–4*, *6* in stereographic pairs)

FIGS. *1*, *3*—*Coosia willowensis* Nelson, n. sp. *1*, Holotype; cranidium, ×1.5, T6550a, F-1.1. *3*, Paratype; pygidium, ×1.5, T6550b, F-1.1, *Crepicephalus* zone. (p. 771)

2, *4*—*Coosia willowensis*, var. A. *2*, Syntype; cranidium, ×2, T6551b, F-1.1. *4*, Syntype; cranidium, ×2, T6551a, F-1.1, *Crepicephalus* zone. (p. 772)

5, *8*—*Lonchocephalus bunus* Walcott. *5*, Hypotype; cranidium, ×3, T6569a, F-1.8. *8*, Hypotype; pygidium, ×3, T6569b, F-1.8, *Crepicephalus* zone. (p. 772)

6—*Coosia quadrata* Nelson, n. sp. Holotype; cranidium, ×2, T6552a, F-1.5, *Crepicephalus* zone. (p. 771)

7—*Uncaspis unca* (Walcott). Topotype; pygidium, ×3, T6568a, F-1.8, *Crepicephalus* zone. (p. 774)

9—*Terranovella dorsalis* (Hall). Hypotypes; several cranidia, ×2, T6565a, F-1.5, *Crepicephalus* zone. (p. 773)

10, *12*—*Modocia walcotti* Lochman. *10*, Topotype; free cheek, ×2, T6566b, F-1.8. *12*, Topotype; cranidium, ×2, T6566a, F-1.8, *Crepicephalus* zone. (p. 773)

11—*Lonchocephalus chippewaensis* Owen. Hypotypes; several cranidia and pygidia, ×2, T6564a, F-30.3, *Crepicephalus* zone. (p. 772)

13—*Millardia optata* (Hall). Hypotype; cranidium, ×3, T6567a, F-1.8, *Crepicephalus* zone. (p. 773)

14—*Aphelaspis depressa* (Shumard). Hypotype; cranidium, ×3, T6570a, F-1.13, *Aphelaspis* zone. (p. 774)

of Minnesota who painstakingly supervised this study and whose criticisms and suggestions were invaluable. The help of Robert Berg in taking some of the photographs and in valuable correspondence is gratefully acknowledged. Appreciations are expressed to Dr. Christina Lochman Balk for helpful suggestions and to Oliver Feniak, V. E. Kurtz and A. R. Palmer for many stimulating discussions on associated faunal and stratigraphic problems. Thanks are also due to Dr. Norman Newell of the American Museum of Natural History, Dr. G. Arthur Cooper of the U. S. National Museum and Dr. L. M. Cline of the University of Wisconsin for the loans of several type specimens, and to Dr. G. M. Schwartz, Director of the Minnesota Geological Survey, for field expenses.

STRATIGRAPHY

It is not the purpose of this paper to propose modifications of the present nomenclature of the Upper Cambrian in the Upper Mississippi Valley. More than 90 years have passed, however, since the earliest investigations in this area and because considerable controversy still exists, a brief consideration of some stratigraphic problems is desirable. Stratigraphic studies are now being conducted east of the St. Croix valley in the hope that solutions may be reached.

Formation names for the lower half of the section in Wisconsin and Minnesota are now generally agreed upon. The Dresbach formation is recognized as the oldest unit. It is divided into three members, the basal coarse-grained Mt. Simon sandstone, the fine-grained Eau Claire sandstone and shale, and the overlying medium-grained Galesville sandstone.

The Dresbach is succeeded by the Franconia formation, consisting of more or less glauconitic sandstone. There is general agreement regarding its subdivision into members but unfortunately these members are now defined mainly on the basis of fossils. Thus the lowest or Ironton member includes all beds containing the *Elvinia* fauna and thus is an expansion of the original Ironton (Ulrich, 1924, p. 93) which combines the coarse basal sand with the overlying glauconite beds. The Goodenough member (Taylors Falls of Stauffer, Schwartz and Thiel, 1939), identified by the *Conaspis* fauna, in the St. Croix valley consists of fine-grained, micaceous sandstone with subordinate glauconitic sandstone. The Hudson member, coinciding with the *Ptychaspis-Prosaukia* zone, includes much fine-grained micaceous sandstone but also part of the overlying sandstone with worm burrows and glauconite. In the absence of fossils the upper part of this last lithologic unit has been termed the Bad Axe member (Stauffer and Thiel, 1941, pp. 205, 206), and it is the youngest division of the Franconia formation. Locally it contains the *Dikelocephalus postrectus* fauna.

Such a subdivision cannot be considered a valid rock stratigraphic classification which should be based on the four fairly widespread lithologic units recognized within the Franconia in the St. Croix valley. They are, from the base upward: coarse-grained non-glauconitic sandstone, fine-grained highly glauconitic sandstone, fine-grained micaceous and slightly glauconitic sandstone, and alternating worm-burrowed glauconitic sandstone and non-glauconitic dolomitic sandstone. To avoid confusion, member names are not used in the following discussion and only the faunal zones are referred to.

Cambrian strata above the Franconia have been variously subdivided and named. All previous writers have recognized the main lithologic units which consist of a basal dolomite, fine-grained dolomitic siltstone, and an upper thick sandstone. Twenhofel, Raasch and Thwaites (1935, p. 1690) and Bridge (1937, p. 234) considered these to be members of the Trempealeau formation. Trowbridge and Atwater (1934, p. 61) and Stauffer, Schwartz and Thiel (1939, p. 1228) referred the dolomite and overlying siltstone to the St. Lawrence formation, and the sandstone at the top to the Jordan formation. The St. Lawrence and Jordan have long been accepted as formations in Minnesota. This latter arrangement seems preferable in the St. Croix valley as the post-Franconia sediments lend themselves readily to a two-fold subdivision. The basal St. Lawrence dolomite is very thin or missing and most of the formation consists of dolomitic siltstone. This is a natural stratigraphic unit, bounded below by the highly

variable glauconitic sandstone of the upper Franconia, and above by the fine sand of the Jordan. The Jordan is easily the most recognizable *lithologic* unit in the St. Croix valley.

The classification adopted in the present paper is, therefore, as follows:

Jordan Formation
  medium-grained sandstone
  fine-grained sandstone (Norwalk of some authors)
St. Lawrence Formation
  dolomitic siltstone (Lodi of some authors)
  dolomite (very thin or absent)
Franconia Formation
  highly variable sandstone
  fine-grained micaceous and non-glauconitic sandstone
  fine-grained highly glauconitic sandstone
  coarse-grained sandstone (Ironton, as defined by Ulrich, 1924, p. 93)
Dresbach Formation
  Galesville member
  Eau Claire member
  Mt. Simon member

PALEONTOLOGY

Trilobites are generally restricted to the finer-grained sediments of the St. Croix valley and these strata are locally extremely fossiliferous. The fossils are predominantly cranidia, pygidia, and a relatively few isolated free cheeks. Only two reasonably complete carapaces have been found.

DRESBACH FORMATION

Three Dresbach faunal zones have been recognized over most of North America (Howell et al., 1944, p. 994). They are in ascending order the *Cedaria*, *Crepicephalus* and *Aphelaspis* zones. Only the upper two, occurring within the Eau Claire member, are exposed in the St. Croix area.

The *Crepicephalus* fauna occurs in the Hudson, Wisconsin region in fine-grained and shaly sandstone at Little Falls Dam (loc. 1) and in dark shales at St. Croix Falls, Wisconsin (loc. 30). It includes the following species:

Coosia quadrata Nelson, n. sp.
Coosia willowensis Nelson, n. sp.
Coosia willowensis, var. A
Lonchocephalus bunus Walcott
Lonchocephalus chippewaensis Owen
Millardia optata (Hall)
Modocia walcotti Lochman
Terranovella dorsalis (Hall)
Uncaspis unca (Walcott)

The *Aphelaspis* zone is known only from Little Falls Dam, Wisconsin (loc. 1) and Nigger Coulee, Wisconsin (loc. 3) where a small fauna consisting only of *Aphelaspis depressa* (Shumard) and *Raaschella* cf. *ornata* Lochman occurs in fine-grained sandstone.

FRANCONIA FORMATION

The Franconia formation has been divided into six faunal zones (Howell et al., 1944, p. 994) which are from the base upward: the *Elvinia*, *Ptychopleurites*, *Conaspis*, *Ptychaspis-Prosaukia*, *Briscoia* and *Dikelocephalus postrectus* zones. In the St. Croix valley only the *Elvinia*, *Conaspis* and *Ptychaspis-Prosaukia* zones are recognized.

The *Elvinia* fauna is restricted to the coarse basal sand (Ironton) and the overlying glauconitic beds but has also been found in the basalt boulder conglomerate at Taylors Falls, Minnesota (loc. 26), in association with an abundant gastropod fauna described by Berkey (1898, p. 279). This fauna contains the following trilobite species:

Berkeia typica Resser
Camaraspis convexa (Whitfield)
Camaraspoides berkeyi (Resser)
Cheilocephalus st. croixensis Berkey
Elvinia roemeri (Shumard)

The *Conaspis* zone comprises the uppermost part of the lower glauconitic beds and much of the overlying fine-grained micaceous sandstone. It is especially well developed in the vicinity of Franconia and Taylors Falls, Minnesota. (locs. 16, 17, 18 and 24). The lower part at these localities is characterized by species of *Parabolinoides* and a few fragmentary *Eoorthis* specimens and represents the *Eoorthis* subzone (Howell et al., 1944, p. 994).

The *Conaspis* zone contains the following species:

Conaspis perseus (Hall)
Croixana n. gen. *bipunctata* (Shumard)
Parabolinoides expansa Nelson, n. sp.
Parabolinoides parallela Nelson, n. sp.
Pseudagnostus josephus (Hall)
Taenicephalus altus Nelson, n. sp.
Taenicephalus shumardi (Hall)
Wilbernia halli Resser
Wilbernia halli var. A

The *Ptychaspis-Prosaukia* zone has been divided by Howell et al. (1944, p. 994) into the *Ptychaspis* and *Prosaukia* subzones.

Collections from the St. Croix valley and contemporary studies in southeastern Minnesota (Feniak, 1948) indicate that in this region three distinct faunules can be recognized in the former. They are characterized from the base upward by *Stigmacephalus oweni*, *Ptychaspis granulosa* and *P. striata*. The last has not been recognized in the St. Croix valley. The *Prosaukia* subzone contains *Ptychaspis miniscaensis* in addition to species of *Prosaukia*.

The *Stigmacephalus oweni* faunule, characterized by several variants of this species all of which are restricted to this subdivision, occurs in fine-grained non-glauconitic sandstone. The species present are:

Eoptychaspis cylindricus Nelson, n. gen., n. sp.
Eoptychaspis cylindricus var. A
Idahoia hera (Walcott)
Monocheilus anatinum (Hall)
Pseudagnostus josepha (Hall)
Ptychaspis arcolensis Nelson, n. sp.
Stigmacephalus oweni (Hall)
Stigmacephalus oweni var. A
Stigmacephalus oweni var. B
Wilbernia diademata (Hall)
Wilbernia explanata (Whitfield)
Wilbernia pero (Walcott)

The *Ptychaspis granulosa* faunule is marked by the presence of this distinctive species. No other trilobite is unique to it in the St. Croix valley, and several range into it from below. This faunule also occurs in the nonglauconitic part of the Franconia. The species present are:

Monocheilus anatinum (Hall)
Pseudagnostus josepha (Hall)
Ptychaspis granulosa (Owen)
Wilbernia explanata (Whitfield)

The *Prosaukia* subzone is characterized by the appearance of *Ptychaspis miniscaensis* and *Prosaukia*. Two faunules have been distinguished within it in the St. Croix valley, a *Ptychaspis miniscaensis* faunule in the upper glauconitic and burrowed sandstone of the Franconia, and a *Prosaukia curvicostata* faunule in the highest dolomitic sandstone beds of this formation.

The *Ptychaspis miniscaensis* faunule contains the following species:

Chariocephalus whitfieldi Hall
Prosaukia cf. *dubia* Ulrich & Resser
Prosaukia cf. *misa* (Hall)
Pseudagnostus josepha (Hall)
Ptychaspis miniscaensis (Owen)
Stigmaspis hudsonensis Nelson, n. gen., n. sp.

The *Prosaukia curvicostata* faunule is known only at Marine (locs. 28, 29) and Stillwater, Minnesota (loc. 21). This species, described by Ulrich and Resser, is the only recognizable fossil that it contains.

The ranges of trilobite genera in the Franconia formation of the St. Croix valley are shown in table 1.

ST. LAWRENCE AND JORDAN FORMATIONS

The post-Franconia sediments in the St. Croix valley constitute the Trempealeauan stage. They have been divided (Howell et al., 1944, pl. 1) into four zones which, from the base upward, are the *Platycolpus-Scaevogyra*, upper *Dikelocephalus*, *Saukiella-Calvinella* and *Plethopeltis* zones. Of these, only the upper *Dikelocephalus* zone can be recognized with assurance in the St. Croix valley.

Generally in the Upper Mississippi valley the *Platycolpus-Scaevogyra* and upper *Dikelocephalus* faunas occur in the lower dolomite and in the siltstone members of the St. Lawrence formation, respectively. The former has not been discovered in the St. Croix valley.

The upper *Dikelocephalus* fauna is present at Afton (locs. 35, 35a) and Stillwater, Minnesota (locs. 21, 22) and is especially characterized by *Dikelocephalus gracilis*. It contains the following species:

Calvinella wisconsinensis Ulrich & Resser
Dikelocephalus gracilis Ulrich & Resser
Dikelocephalus granosus Ulrich & Resser
Dikelocephalus hotchkissi Ulrich & Resser
Dikelocephalus minnesotensis Owen
Dikelocephalus ovatus Ulrich & Resser
Dikelocephalus oweni Ulrich & Resser
Illaenurus calvini Walter
Tellerina crassimarginata (Whitfield)

The *Osceolia* fauna (Howell et al., 1944, p. 997) occurs in the St. Lawrence siltstone at Osceola (loc. 37) and in the overlying Jordan sandstone at Marine (loc. 28) and Osceola, Wisconsin (locs. 37, 37a). It includes the following species:

Acheilops sp.
"Agnostus" disparilis (Hall)
Bowmania sp.
Corbinia sp.
Dikelocephalus halli Ulrich & Resser
Dikelocephalus thwaitesi Ulrich & Resser
Eurekia binodosa (Hall)
Illaenurus quadratus Hall
Osceolia obsoleta reversa Ulrich & Resser

Osceolia osceola (Hall)
Osceolia separata Ulrich & Resser
Plethometopus convexus (Whitfield)
Saukiella norwalkensis Ulrich & Resser
Saukiella pyrene (Walcott)
Stenopilus sp.
Tellerina leucosia (Walcott)
Triarthropsis sp.

In 1939 Raasch (p. 104) considered the siliferous sandstone at Osceola (loc. 37) is not seen in contact with the Lodi silts. Most of the collections came from abandoned quarries north of town and Raasch (personal communication, Feb. 3, 1950) believes that the quarry beds are the leached equivalents of the dolomitic siltstones which contain fragmentary fossils in the town of

TABLE 1.—RANGES OF TRILOBITE GENERA IN THE FRANCONIA FORMATION OF THE ST. CROIX VALLEY

(The dashed line indicates an indefinite boundary because of unfossiliferous strata at this position)

Genus	*Elvinia* zone	*Conaspis* zone	*Ptychaspis-Prosaukia* zone		
			Ptychaspis subzone		*Prosaukia* subzone
			Stigmacephalus oweni faunule	*P. granulosa* faunule	
Berkeia[1]	******				
Camaraspis	**********				
Camaraspoides[1]	******				
Cheilocephalus[1]	******				
Elvinia	**********				
Conaspis		*********			
Croixana		**********			
Parabolinoides		*********			
Taenicephalus		**********			
Pseudagnostus		**********	**********	**********	******
Wilbernia		**********	**********	*******	
Eoptychaspis			**********		
Idahoia			**********		
Monocheilus			**********	**********	
Stigmacephalus			**********		
Ptychaspis			**********	**********	********
P. arcolensis			**********		
P. granulosa				**********	
P. miniscaensis					*******
Stigmaspis					******
Chariocephalus					**********
Prosaukia					**********

[1] Restricted to the boulder conglomerate at Taylors Falls, Minn. (loc. 26).

sandstone bearing this fauna at Osceola and elsewhere in Wisconsin (p. 108) as a facies of the upper *Dikelocephalus* zone, and thus (in his terminology) a part of the Lodi member of the Trempealeau formation. Earlier, Sardeson (1903, p. 475; 1932, p. 105) and Walcott (1914, p. 356) had considered these beds to be part of the upper St. Lawrence. At present, Raasch (personal communication, Feb. 3, 1950) considers them to be part of the Arcadia member (Howell et al., 1944, p. 997) which lies well below the upper *Dikelocephalus* zone.

The major part of the fine-grained fos-

Osceola. However, the occurrence of several feet of the sandstone overlying the silts in Osceola, a plane table survey by C. R. Stauffer connecting the sections within the town and at the quarries, and the good exposures at Osceola bridge (loc. 37a) seem to show clearly that this interpretation is not correct and the quarry sandstone overlies the siltstone in Osceola.

The *Osceolia*-bearing sandstone at Osceola in the past has been referred to the Lodi and Arcadia members of the upper St. Lawrence formation. In the author's opinion this is the basal portion of the thick, continuously

deposited sandstone of the Jordan formation. Except for local pebble beds within the basal sands at Osceola bridge, there is no suggestion of lithologic discontinuity between the top of the underlying siltstone and the base of the Ordovician dolomite.

The recording by Stauffer and Thiel (1941, p. 133) of the upper *Dikelocephalus* fauna from the "Lodi" siltstone underlying

FIG. 1—Cambrian fossil localities in the St. Croix valley.

the *Osceolia*-bearing (Norwalk) sandstone in the Osceola bridge section appears to be contrary to fact.

Except at Osceola and Marine (loc. 28) fossils are not abundant in the Jordan sandstone of the St. Croix valley. Collections from Afton (loc. 35), Stillwater (loc. 21) and Marine, Minnesota (loc. 29) probably came from the *Saukiella-Calvinella* zone. These localities yield the following species:

Acheilops sp.
Bowmania sp.
Calvinella spiniger (Hall)
Corbinia sp.
Saukia imperatrix Ulrich & Resser
Saukiella sp.
Tellerina sp.

The *Plethopeltis* zone, present in the Madison formation of eastern Wisconsin, has not been found in the St. Croix valley.

INDEX OF LOCALITIES

Figure 1 shows the geographic distribution of the fossil localities in the St. Croix valley.

Loc. 1. Little Falls Dam, Wis. At Power Dam on Willow River, 3 miles northeast of Hudson, Wis. *Crepicephalus* and *Aphelaspis* zones of Eau Claire member, Dresbach formation.

Loc. 2. Hudson, Wis. Bluff along south side of town. Upper part of Dresbach and most of Franconia formation.

Loc. 3. Nigger Coulee, Wis. Gulley and roadcut on State Highway 35, 2 miles north of Hudson, Wis. *Aphelaspis* zone of Dresbach formation and *Elvinia*, *Conaspis* and basal part of *Ptychaspis-Prosaukia* zone of Franconia formation.

Loc. 15. Arcola, Minn. Gorge east of Arcola schoolhouse. All of Franconia formation above base of *Ptychaspis-Prosaukia* zone.

Loc. 16. Franconia, Minn. East side of Lawrence Creek, in Daggett's Gulch. Uppermost Dresbach and *Elvinia* and *Conaspis* zones of Franconia formation.

Loc. 17. Franconia, Minn. Type section of Franconia formation along west side of Lawrence Creek. Uppermost Dresbach and *Elvinia* and *Conaspis* zones of Franconia formation.

Loc. 18. Taylors Falls, Minn. Highway cut 1 mile southwest of town. Very thick section of the *Conaspis* zone, Franconia formation.

Loc. 21. Stillwater, Minn. In Boom Hollow and picnic grounds, 1 mile northeast of town. Uppermost Franconia, complete St. Lawrence and Jordan formations.

Loc. 22. Stillwater, Minn. In Fairy Glen, ¼ mile north of town. Complete section of St. Lawrence and Jordan formations.

Loc. 24. Taylors Falls, Minn. Along Pine Point Trail, southwest of town. Upper Dresbach through *Conaspis* zone of Franconia formation.

Loc. 24a. Taylors Falls, Minn. Along Curtain Falls Trail, southwest of town. *Elvinia* and *Conaspis* zones, Franconia formation.

Loc. 26. Taylors Falls, Minn. Conglomerate of basalt boulders at intersection of Mill St. and railroad, southwest edge of town. Contains *Elvinia* fauna.

Loc. 28. Marine, Minn. North of town 1 mile. Franconia formation from base of *Ptychaspis-Prosaukia* zone, and part of Jordan formation.

Loc. 29. Marine, Minn. At Ferry and along Mill Creek. *Conaspis* through *Prosaukia* zones of the Franconia formation; St. Lawrence and lower Jordan covered; upper Jordan sandstone exposed along secondary road at south edge of town.

Loc. 30. St. Croix Falls, Wis. In stream bed, ¼ mile north of Fish Hatchery. *Crepicephalus* zone, Dresbach formation.

Loc. 31. Copas, Minn. Gorge on Sanborn prop-

erty. *Conaspis* zone and all higher Franconia strata.

Loc. 35. Afton, Minn. Along creek at south edge of town. Uppermost Franconia and all of St. Lawrence and Jordan formations.

Loc. 35a. Afton, Minn. Trout Brook, 2 miles southwest of town. Lodi silts of St. Lawrence formation.

Loc. 36. Franconia, Minn. West bank of St. Croix River, 1 mile southwest of town. *Conaspis* zone, Franconia formation.

Loc. 37. Osceola, Wis. Along creek in town, Eagle Point Bluff and roadcut south of town. Uppermost Franconia and complete St. Lawrence and Jordan sections.

Loc. 37a. Osceola Bridge, Minn. Road across St. Croix River from Osceola, Wis. Parts of St. Lawrence and Jordan formations.

SYSTEMATIC DESCRIPTIONS

In the following systematic descriptions and accompanying plates, the specimen numbers, unless otherwise noted, refer to specimens in the Paleontologic Collection, University of Minnesota. The F- numbers refer to the numbered localities (p. 770) and the relative stratigraphic position in each section. For example, F-1.1 refers to the lowest stratigraphic horizon from locality 1, Little Falls Dam, Wisconsin, F-1.2, the next higher horizon, etc. The terminology used in describing the faunas is that suggested by Howell et al. (1947, p. 73), with the addition of the term *frontal area* for the region between the front of the glabella and the anterior margin. The variants described in this paper are regarded as morphologically distinct but intergrading extremes of their respective species.

The stereographic photographs in each of the plates were obtained by a normal vertical camera mount modified so that the mounting rod could be rotated. One view was taken with the camera in a vertical position, and the second with the axis tilted about 10°. This technique was used for illustration of nearly all the new species described in this paper.

CREPICEPHALUS ZONE

Genus COOSIA Walcott, 1911

COOSIA QUADRATA Nelson, n. sp.
Plate 106, figure 6

Cranidium quadrate; glabella convex, tapering, rounded anteriorly, length equal to width; occipital furrow pronounced; occipital ring less than one-fourth length of glabella; dorsal furrow pronounced; brim flat, down-sloping, separated from border by moderate marginal furrow; border sharply uparched and convex, slightly wider than brim; frontal area about one-half length of glabella, gently expanding anteriorly, and not as wide as cranidium at position of palpebral lobes; fixed cheeks gently upsloping, less than one-third glabella width; palpebral lobes small, lying about on midline of glabella; posterior limbs unknown.

Free cheek, thorax and pygidium unknown.

Remarks.—This species differs from *C. willowensis* in the quadrate shape of the cranidium, the more deeply impressed dorsal and occipital furrows, and the nearly equal sized brim and border.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.5.

Holotype.—Cranidium, T6552a.

COOSIA WILLOWENSIS Nelson, n. sp.
Plate 106, figures 1, 3

Glabella convex, tapering, rounded anteriorly, length equal to width; occipital furrow moderate, lacking near dorsal furrow; occipital ring less than one-fifth length of glabella; dorsal furrow moderate; frontal area more than one-half length of glabella, expanding anteriorly, not as wide as cranidium at position of palpebral lobes, divided by a broad shallow marginal furrow into a flat to concave downsloping brim and a gently upsloping convex border; border more than twice the width of brim; fixed cheeks nearly flat, less than one-third glabella width; palpebral lobes small, lying between midline and anterior one-third of glabella; posterior limbs of medium width, length less than that of occipital ring.

Pygidium semicircular in outline, moderately convex; axial lobe tapering, slightly more than one-half of pygidium length and one-fourth pygidium width; margin broad and flat to concave.

Free cheek and thorax unknown.

Remarks.—The broad, shallow marginal furrow and the shape of the frontal area are the distinguishing characteristics of this species.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.1.

Holotype.—Cranidium, T6550a; paratype, pygidium, T6550b.

COOSIA WILLOWENSIS var. A
Plate 106, figures 2, 4

This variant has a more pronounced marginal furrow and a more sharply flexed convex brim and border than the typical form.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach Formation; Little Falls Dam, Wis., F-1.1.

Hypotypes.—Cranidia and pygidia, T6564a.

Syntypes.—Cranidia, T6551a, T6551b.

Genus LONCHOCEPHALUS Owen, 1852
LONCHOCEPHALUS BUNUS Walcott
Plate 106, figures 5, 8

Lonchocephalus bunus WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 190, pl. 34, figs. 9, 9a.

Remarks.—Walcott originally described this species from the Franconia formation at Minneiska, Minnesota. Recent field work in that area and examination of the types has shown that these are from the Dresbach formation and include specimens of *Terranovella dorsalis* as well as *L. bunus* (A. R. Palmer, personal communication, Oct. 17, 1949). Walcott's specimens apparently were mislabeled.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.8.

Hypotypes.—Cranidium, T6569a; pygidium, T6569b.

LONCHOCEPHALUS CHIPPEWAENSIS Owen
Plate 106, figure 11

Lonchocephalus chippewaensis OWEN, 1852, Geol. Survey Wisconsin, Iowa Minnesota Rept., p. 576, table 1, figs. 6, 14, table 1a, fig. 9; WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 190, pl. 34, figs. 3, 3a, pl. 37, fig. D; SHIMER & SHROCK, 1944, Index fossils of North America, p. 627, pl. 256, fig. 30.
Conocephalites chippewaensis SHUMARD, 1863, St. Louis Acad. Sci. Trans., vol. 2, p. 104.
Conocephalites minor HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 149, pl. 8, figs. 1–4.

Remarks.—This species occurs abundantly in soft shales at St. Croix Falls, Wisconsin, where the cranidia are generally

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EXPLANATION OF PLATE 107

Elvinia and *Conaspis* zones—Franconia formation
(Figures *1–4* in stereographic pairs)

FIGS. *1, 3—Parabolinoides expansa* Nelson, n. sp. *1*, Holotype; cranidium, ×1.5, T6553a, F-18.1. *3*, Paratype; free cheek, ×1, T6553b, F-18.1, basal *Conaspis* zone. (p. 776)

2, 4, 7—Taenicephalus altus Nelson, n. sp. *2*, Syntype; cranidium, ×2, T6504a, F-29.1. *4*, Syntype; rubber cast of complete cephalon, ×2, T6504b, F-29.1. *7*, Syntype; free cheek, ×2, T6504c, F-29.1, upper *Conaspis* zone. (p. 777)

5—Pseudagnostus josepha (Hall). Holotype; cranidium, ×3, T6571a, F-16.12, *Conaspis* zone. (p. 776)

6, 14—Camaraspoides berkeyi (Resser). *6*, Topotype; cranidium, ×1.5, T6575a, F-26.1. *14*, Topotype; pygidium, ×1.5, T6575b, F-26.1, *Elvinia* zone. (p. 774)

8—Elvinia roemeri (Shumard). Hypotype; cranidium, ×1, T6574a, F-3.26, *Elvinia* zone. (p. 775)

9, 16—Wilbernia halli, var. A. *9*, Holotype; cranidium, ×1, T6577a, F-16.12. *16*, Paratype; pygidium, rubber cast, ×1.5, T6577b, F-16.12, *Conaspis* zone. (p. 777)

10, 12—Croixana bipunctata (Shumard). *10*, Topotype; free cheek, ×3, T6579b, F-16.12. *12*, Topotype; cranidium, ×3, T6579a, F-16.12, *Conaspis* zone. (p. 775)

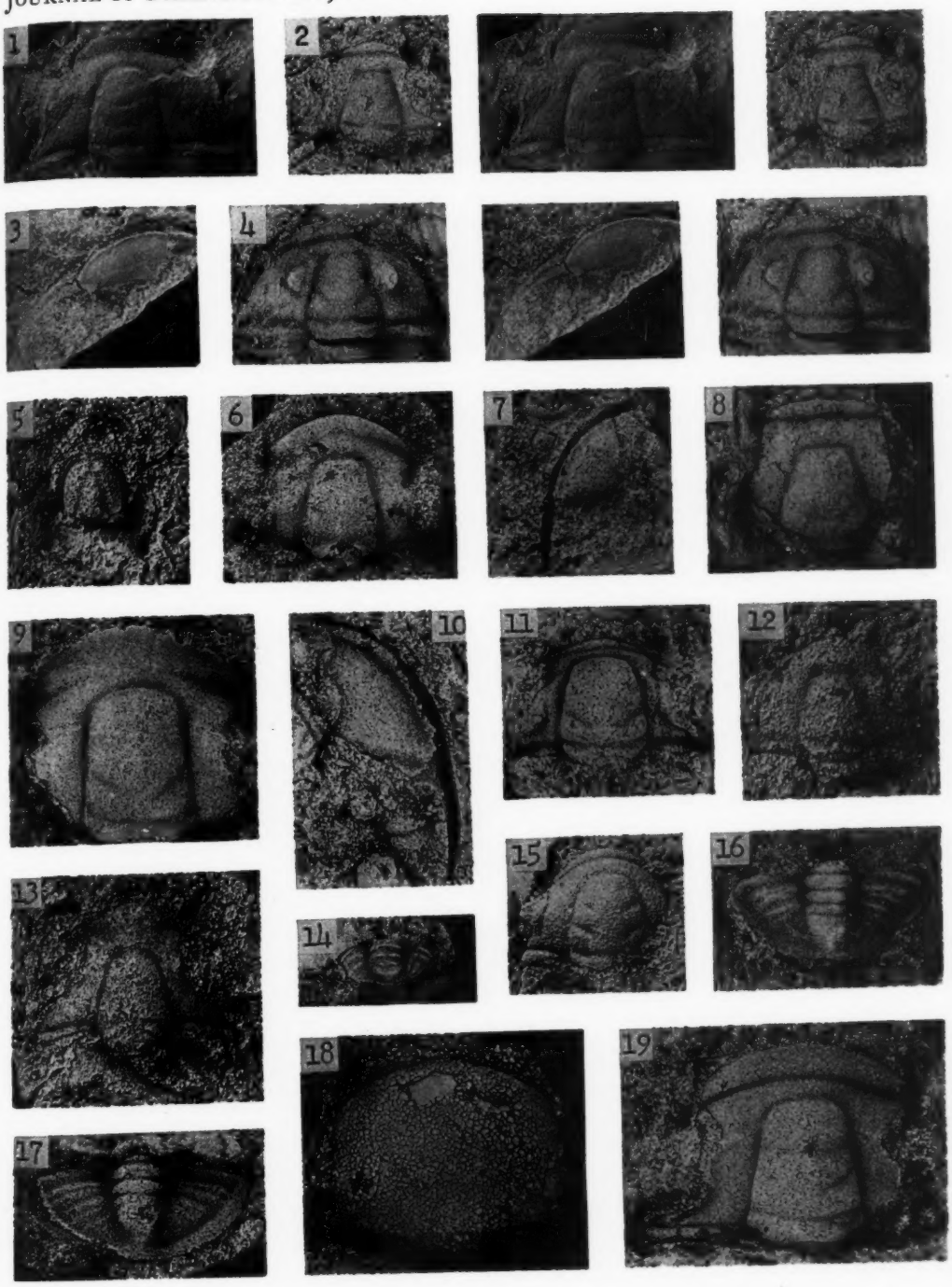
11—Conaspis perseus (Hall). Hypotype; cranidium, ×3, T6578a, F-16.12, *Conaspis* zone. (p. 775)

13—Parabolinoides parallela Nelson, n. sp. Holotype; cranidium, ×2, T6562a, F-24a.8, basal *Conaspis* zone. (p. 776)

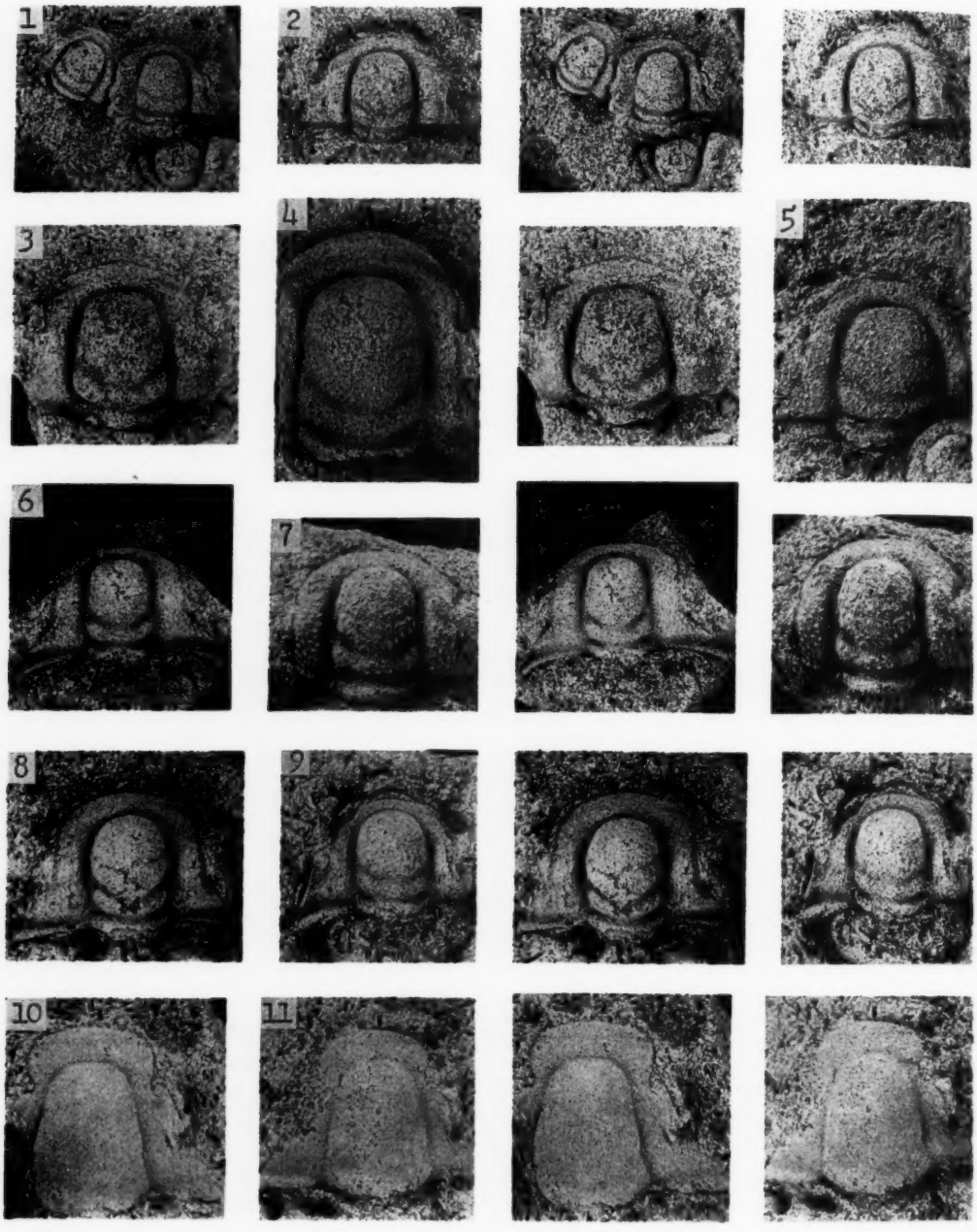
15—Berkeia typica Resser. Holotype; cast of cranidium, ×3, Columbia Univ. No. 22285, F-26.1, *Elvinia* zone. (p. 774)

17, 19—Wilbernia halli Resser. *17*, Topotype; pygidium, ×1.5, T6576b, F-16.12. *19*, Topotype; cranidium, ×1.5, T6576a, F-16.12, *Conaspis* zone. (p. 777)

18—Camaraspis convexa (Whitfield). Hypotype; cranidium, ×1.5, T6573a, F-17.4. [From an old collection, labelled "from type locality of species (*Agraulos hemisphericus* Berkey), Taylors Falls, Minn." The coarse glauconitic sandstone in which this specimen occurs is not present at Taylors Falls, but is found nearby at Franconia, Minnesota (loc. 17). *Elvinia* zone. (p. 774)



Nelson, Cambrian trilobites



Nelson, Cambrian trilobites

flattened. The pygidia are readily distinguishable from those of *L. bunus* by their carinate margins.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; St. Croix Falls, Wis., F-30.3.

Hypotypes.—Cranidia and pygidia, T6564a.

Genus MILLARDIA Walcott, 1916
MILLARDIA OPTATA (Hall)
Plate 106, figure 13

Conocephalites optatus HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 222, pl. 5A, fig. 7.
Ptychoparia optata MILLER, 1889, North American geology and palaeontology, p. 539.
Millardia optata WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 165, pl. 28, figs. 4a–f; LOCHMAN, 1940, Jour. Paleontology, vol. 14, pp. 9, 44.
Menomonia optata RESSER, 1938, Smithsonian Misc. Coll., vol. 97, no. 10, p. 35; LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 75, pl. 4, figs. 30–33.

Remarks.—In assigning *Conocephalites optatus* Hall to *Millardia*, Walcott (1916, p. 165) made use of material from the same locality as the present figured specimen. Resser's suppression of *Millardia* in favor of *Menomonia* (1938, p. 35) was questioned by Lochman (1940, p. 9). The present assignment of the species to *Millardia* is based on the presence of stalked eyes, which are generally broken, and a frontal area somewhat narrower than the maximum glabella width.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.5, 1.8.

Hypotype.—Cranidium, T6567a.

Genus MODOCIA Walcott, 1924
MODOCIA WALCOTTI Lochman
Plate 106, figures 10, 12

Crepicephalus unca WALCOTT (part), 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 217, figs. 1a–c, not figs. 1e, d.
Uncaspis unca KOBAYASHI (part), 1935, Imp. Univ. Tokyo Jour. Fac. Sci., ser. 2, vol. 4, pt. 2, p. 279.
Modocia walcotti LOCHMAN, 1943, Jour. Paleontology, vol. 17, p. 233, pl. 35, figs. 1, 2.

Remarks.—The illustrated specimens are topotypes which occurred associated with pygidia of *Uncapis unca* (Walcott).

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.5, 1.8.

Topotypes.—Cranidium, T6566a; free cheek, T6566b.

Genus TERRANOVELLA Lochman, 1938
TERRANOVELLA DORSALIS (Hall)
Plate 106, figure 9

Conocephalites? (Arionellus?) dorsalis HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 222.
Ptychoparia dorsalis VOGDES, 1890, U. S. Geol. Survey Bull. 63, p. 141; TELLER, 1911, Wisconsin Nat. History Soc. Bull., vol. 9, no. 4, p. 267.
Lonchocephalus sospita WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 195, pl. 36, figs. 1, 1a (Raasch, personal communication, Feb. 3, 1950).
Terranovella dorsalis RAASCH & LOCHMAN, 1943, Jour. Paleontology, vol. 17, p. 234, pl. 35, figs. 3–10, 17.

Remarks.—This species is generally uncommon in the St. Croix valley but is abundant at one locality. It is characterized by the tapering, truncate glabella, deeply im-

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EXPLANATION OF PLATE 108

Ptychaspis-Prosaukia zone
Stigmacephalus oweni faunule—Franconia formation
(Figures *1–3*, *6–11* in stereographic pairs)

FIGS. *1–5*—*Eoptychaspis cylindricus* Nelson, n. sp. *1*, Syntype; three cranidia, ×1.5, T6554a, F-29.6. *2*, Syntype; cranidium, ×1.5, T6554b, F-29.6. *3*, Syntype; cranidium, ×2, T6554d, F-29.5. *4*, Syntype; cranidium, ×2, T6554c, F-29.5. *5*, Syntype; cranidium, ×2, T6554e, F-29.6. (p. 778)

6, *7*—*Ptychaspis arcolensis* Nelson, n. sp. *6*, Holotype; cranidium, ×2, T6556a, F-15.1. *7*, Paratype; cranidium, ×1.5, T6556b, F-15.4. (p. 779)

8, *9*—*Eoptychaspis cylindricus*, var. A. *8*, Holotype; cranidium, ×2, T6557a, F-29.5. *9*, Paratype; cranidium, ×2, T6557b, F-29.5. (p. 778)

10, *11*—*Stigmacephalus oweni* (Hall), var. B. *10*, Holotype; cranidium, ×2, T6558a, F-29.3. *11*, Paratype; cranidium, ×2, T6558b, F-29.3. (p. 780)

pressed dorsal furrow, and the lack of a marginal furrow.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.5.

Hypotypes.—Cranidia, T6565a.

Genus UNCASPIS Kobayashi, 1935, emended
UNCASPIS UNCA (Walcott)
Plate 106, figure 7

Crepicephalus unca WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 217, pl. 35, figs. 1e, d (not figs. 1, 1a–c).
Uncaspis unca KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, p. 279; RAASCH & LOCHMAN, 1943, Jour. Paleontology, vol. 17, p. 223, pl. 34, figs. 1–5; SHIMER & SHROCK, 1944, Index fossils of North America, p. 635, pl. 266, figs. 26, 27 (not fig. 25).

Remarks.—Unfortunately, only pygidia of this species have been found at this locality, where they occur with cranidia of *Modocia walcotti*. This apparently led Walcott to assume that the two parts belong to one species.

Occurrence.—*Crepicephalus* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.8.

Topotype.—Pygidium, T6568a.

APHELASPIS ZONE
Genus APHELASPIS Resser, 1935
APHELASPIS DEPRESSA (Shumard)
Plate 106, figure 14

Conocephalites depressus SHUMARD, 1861, Am. Jour. Sci., 2d ser., vol. 32, p. 219.
Ptychoparia depressa MILLER, 1889, North American geology and palaeontology, p. 565.
Aphelaspis depressa RESSER, 1935, Smithsonian Misc. Coll., vol. 93, no. 5, p. 11; BRIDGE & GIRTY, 1936, U. S. Geol. Survey Prof. Paper 186-M, p. 255, pl. 69, figs. 23–26.
Aphelaspis depressus SHIMER & SHROCK, 1944, Index fossils of North America, p. 619, pl. 263, figs. 35, 36.

Remarks.—Exposures of the *Aphelaspis* zone in the St. Croix valley are confined to the Hudson, Wis. region, where this species is associated with *Raaschella* cf. *ornata* Lochman.

Occurrence.—*Aphelaspis* zone, Eau Claire member, Dresbach formation; Little Falls Dam, Wis., F-1.10, 1.12, 1.13; Nigger Coulee, Wis., F-3.2, 3.3, 3.4.

Hypotype.—Cranidium T6570a.

ELVINIA ZONE
Genus BERKEIA Resser, 1937
BERKEIA TYPICA Resser
Plate 107, figure 15

Agraulos convexus var. B. BERKEY, 1898, Am. Geologist, vol. 21, p. 288, pl. 20, figs. 5, 6.
Berkeia typica RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 3.

Remarks.—This species occurs in a marginal conglomerate facies near hills of pre-Cambrian basalt. It is generally associated there with *Camaraspoides berkeyi* and many gastropods.

Occurrence.—*Elvinia* zone, Mill St. conglomerate; Taylors Falls, Minn., F-26.1.

Holotype.—Cranidium, Columbia Univ. no. 22285.

Genus CAMARASPIS Ulrich & Resser
(in Ulrich, 1924)
CAMARASPIS CONVEXA (Whitfield)
Plate 107, figure 18

Arionellus (Agraulos) convexus WHITFIELD, 1878, Wisconsin Geol. Survey Ann. Rept. 1877, p. 57.
Arionellus convexus WHITFIELD, 1882, Geology of Wisconsin, vol. 4, p. 190, pl. 1, fig. 17.
Agraulos hemisphericus BERKEY, 1898, Am. Geologist, vol. 21, p. 289, pl. 20, figs. 14, 15.
Camaraspis convexus ULRICH, 1924, Wisconsin Acad. Sci., Arts and Letters, vol. 21, p. 94.
Camaraspis convexa FREDERICKSON, 1948, Jour. Paleontology, vol. 22, p. 798, pl. 123, figs. 12, 13 (for synonymy to date); WILSON, 1949, idem, vol. 23, p. 33, pl. 10, figs. 6, 8, 11.

Remarks.—This species is rare in the St. Croix valley but it ranges through most of the *Elvinia* zone and is fairly abundant elsewhere in the Upper Mississippi valley. It is found in coarse sand at the base of the Franconia formation and in the overlying glauconitic beds.

Occurrence.—*Elvinia* zone, Franconia formation; Franconia, Minn., F-17.4; Nigger Coulee, Wis., F-3.26.

Hypotype.—Cranidium, T6573a.

Genus CAMARASPOIDES Frederickson, 1949
CAMARASPOIDES BERKEYI (Resser)
Plate 107, figures 6, 14

Agraulos convexus BERKEY, 1898, Am. Geologist, vol. 21, p. 288, pl. 20, figs. 9–11, pl. 21, figs. 3, 7.
Agraulos convexus var. A. BERKEY, 1898, Am. Geologist, vol. 21, p. 288, pl. 20, figs. 1, 2, pl. 21, fig. 5 (the holotype designated by Resser).

Modocia berkeyi RESSER, 1935, Smithsonian Misc. Coll., vol. 93, no. 5, p. 42.
Camaraspoides berkeyi FREDERICKSON, 1949, Jour. Paleontology, vol. 23, p. 349, pl. 68, figs. 1–9.

Remarks.—This species is restricted, in the St. Croix valley, to the conglomerates at Taylors Falls. It is the species designated by Frederickson as the genotype of *Camaraspoides*.

Occurrence.—*Elvinia* zone, Mill St. conglomerate; Taylors Falls, Minn., F-26.1.

Topotypes.—Cranidium, T6575a; pygidium, T6575b.

Genus ELVINIA Walcott, 1924
ELVINIA ROEMERI (Shumard)
Plate 107, figure 8

Dikelocephalus roemeri SHUMARD, 1861, Am. Jour. Sci., 2d ser., vol. 32, p. 220.
Ptychoparia roemeri WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 352.
Elvinia roemeri WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 56, pl. 11, fig. 3; ——, 1924, idem, vol. 75, no. 3, p. 88, pl. 17, figs. 9–13; FREDERICKSON, 1949, Jour. Paleontology, vol. 23, p. 352, pl. 69, figs. 19–21 (for synonymy to date); LOCHMAN, 1950, idem, vol. 24, p. 333, pl. 47, figs. 21–23.

Remarks.—This species is rare in the St. Croix valley where it is restricted to the lower glauconitic beds of the Franconia formation.

Occurrence.—*Elvinia* zone, Franconia formation; Hudson, Wis., F-2.15; Nigger Coulee, Wis., F-3.26.

Hypotype.—Cranidium, T6574a.

CONASPIS ZONE

Genus CONASPIS Hall, 1863
CONASPIS PERSEUS (Hall)
Plate 107, figure 11

Conocephalites perseus HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 153, pl. 7, figs. 17–23, pl. 8, fig. 33.
Conaspis perseus HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 152; WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357; RESSER, 1937, idem, vol. 95, no. 22, p. 7; SHIMER & SHROCK, 1944, Index fossils of North America, p. 621, pl. 263, fig. 27.
Ptychoparia perseus MILLER, 1889, North American geology and palaeontology, p. 565.

Remarks.—This species is very abundant in the vicinity of Franconia and Taylors Falls. It is the only species now referred to *Conaspis*.

Occurrence.—*Conaspis* zone, Franconia formation; Franconia, Minn., F-16.12, 17.12, 17.14, 17.15, 17.16, 17.20, 36.7, 36.8; Taylors Falls, Minn., F-18.13, 18.14, 18.15, 18.16, 24.16.

Hypotype.—Cranidium, T6578a.

Genus CROIXANA Nelson, n. gen.

Glabella cuneiform, moderately convex; dorsal furrow with anterior pits; frontal area convex, pointed to rounded, abruptly downturned along anterior margin; fixed cheeks about one-half width of glabella; palpebral lobes small, on anterior one-third line of glabella.

Genotype.—*Arionellus bipunctatus* Shumard.

Remarks.—The important generic features of *Croixana* are the convex and pointed to rounded frontal area abruptly downturned along the anterior margin, and the anterior pits.

Resser (1937, p. 25) proposed the genus *Stigmacephalus* to include *Conocephalites oweni* Hall, the genotype, and *Arionellus bipunctatus* Shumard, but the writer considers these species to be generically distinct.

Croixana differs from *Taenicephalus* in the somewhat smaller palpebral lobes, generally less well impressed dorsal furrow, and the lack of glabellar furrows and marginal furrow.

Occurrence.—*Conaspis* zone, Franconia formation.

CROIXANA BIPUNCTATA (Shumard)
Plate 107, figures 10, 12

Arionellus bipunctatus SHUMARD, 1862, St. Louis Acad. Sci. Trans., vol. 2, p. 101; HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 169, pl. 7, figs. 50, 51.
Agraulus bipunctatus MILLER, 1889, North American geology and palaeontology, p. 527.
Conaspis bipunctata WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, pp. 357–358.
Stigmacephalus bipunctatus RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 26.
Taenicephalus bipunctatus STAUFFER & THIEL, 1941, Minnesota Geol. Survey Bull. 29, p. 248.

Remarks.—This species is very abundant in the *Conaspis* zone, and is especially common at Franconia, Minn. The specimens from this area show considerable diversity and may include several variants. They are, however, generally poorly preserved and the described features of *Croixana* are based in part on specimens from southern Minnesota.

Occurrence.—*Conaspis* zone, Franconia formation; Marine, Minn., F-29.1; Franconia, Minn., F-16.12, 17.15, 17.16, 36.6, 36.7, 36.8; Taylors Falls, Minn., F-18.11, 18.15, 18.16, 24.16.

Topotypes.—Cranidium, T6579a; free cheek, T6579b.

Genus PARABOLINOIDES Frederickson, 1949
PARABOLINOIDES EXPANSA Nelson, n. sp.
Plate 107, figures 1, 3

Glabella conoid in outline, slightly convex, tapered, rounded anteriorly, length equal to width; two very weak glabellar furrows, crossing glabella, oblique at sides; occipital furrow moderate; occipital ring about one-fifth of length of glabella; dorsal furrow moderate; frontal area about one-half length of glabella, sharply expanding anteriorly, wider than cranidium at position of palpebral lobes; brim convex, downsloping, separated from equal sized nearly flat border by moderate marginal furrow; fixed cheeks flat, one-fourth width of glabella; palpebral lobes small, lying about on anterior one-fourth line of glabella; posterior limbs wide, triangular, length slightly less than that of occipital ring.

Free cheek nearly flat, more convex near marginal furrow; border narrow; bearing long curved spine.

Thorax and pygidium unknown.

Remarks.—*Parabolinoides expansa* is similar to *P. contractus* Frederickson, the genotype of *Parabolinoides*. It differs, however, in the convex, downsloping brim and flat border as opposed to the flat brim and convex, raised border in *P. contractus*. The arrangement and number of the glabellar furrows are different in the two species, but this may be due largely to the poor preservation of these features in *P. expansa*.

Many specimens of this type apparently have been assigned by workers in the Upper Mississippi Valley to Raasch's invalid genus *Maustonia*. Frederickson does not, however, regard "*Maustonia*" *nasuta* (the genotype as implied by Raasch, 1939, p. 94) as a species of *Parabolinoides*.

Occurrence.—Lower *Conaspis* zone (*Eoorthis* subzone), Franconia formation; Taylors Falls, Minn., F-18.1.

Holotype.—Cranidium, T6553a; paratype, free cheek, T6553b.

PARABOLINOIDES PARALLELA Nelson, n. sp.
Plate 107, figure 13

Glabella conoid, slightly convex, tapered, rounded anteriorly, length equal to width; occipital furrow moderate; occipital ring about one-fourth length of glabella; dorsal furrow moderate; frontal area about two-thirds length of glabella, made up of downsloping flat brim having parallel lateral margins and an equally sized slightly upsloping triangular and pointed border; brim and border separated by shallow marginal furrow; fixed cheeks flat, one-fourth to one-third width of glabella; palpebral lobes small, lying on anterior one-fourth line of glabella; posterior limbs wide, triangular, length slightly less than that of occipital ring.

Free cheek, thorax and pygidium unknown.

Remarks.—This species differs from *Parabolinoides expansa* in possessing a larger frontal area and having a brim with parallel lateral margins as opposed to the marked expansion of the brim in the latter. Glabellar furrows are not visible on the specimens, but this may be due to the preservation.

Occurrence.—Lower *Conaspis* zone (*Eoorthis* subzone), Franconia formation; Taylors Falls, Minn., F-24.7, 24a.8.

Holotype.—Cranidium, T6562a.

Genus PSEUDAGNOSTUS Jaekel, 1909
PSEUDAGNOSTUS JOSEPHA (Hall)
Plate 107, figure 5

Agnostus josepha HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 178, pl. 6, figs. 54, 55.

Pseudagnostus josepha KOBAYASHI, 1935, Imp. Univ. Tokyo, sec. 2, vol. 4, pt. 2, p. 108; ——, 1935, idem, vol. 5, pt. 5, p. 157; SHIMER & SHROCK, 1944, Index fossils of North America, p. 601, pl. 251, figs. 5, 6; FREDERICKSON, 1949, Jour. Paleontology, vol. 23, p. 362, pl. 72, fig. 17; LOCHMAN, 1950, idem, vol. 24, p. 329, pl. 46, fig. 14.

Remarks.—This species occurs through most of the *Conaspis* zone and a major portion of the *Ptychaspis-Prosaukia* zone, but few specimens are well preserved. The head shield is characterized by a triangular galbella and a median furrow extending to the front margin. Several poorly preserved pygidia have been found, but no thoracic segments are known from this area.

Occurrence.—*Conaspis* zone, Franconia formation; Hudson, Wis., F-2.17a; Franconia, Minn., F-16.12. *Ptychaspis-Prosaukia* zone, *Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.18; Marine, Minn., F-29.5. *Ptychaspis miniscaensis* faunule, Franconia formation; Afton, Minn., F-35.1.

Hypotype.—Cranidium, T6571a.

Genus TAENICEPHALUS Ulrich & Resser (in Walcott, 1924)

TAENICEPHALUS ALTUS Nelson, n. sp.

Plate 107, figures 2, 4, 7

Taenicephalus shumardi WALCOTT (part), 1925, Smithsonian Misc. Coll., vol. 75, no. 3, pl. 17, fig. 15 (fide Raasch).

Cranidium with high relief. Glabella cuneiform, length equal to width; two pairs of faint glabellar furrows, anterior pair slightly oblique, posterior pair at about 45°; occipital furrow wide; occipital ring slightly wider at center than at sides; dorsal furrow deep, with two anterior pits; brim strongly convex, width slightly less than one-half length of glabella; marginal furrow deep, of medium width; border less than one-half width of brim; fixed cheeks about one-fifth width of glabella; palpebral lobes on anterior one-third line of glabella, elevated high above rest of cranidium; posterior limbs of medium width, length equal to that of occipital ring.

Free cheek with ocular platform moderately convex, flat immediately adjacent to eye; marginal furrow generally shallow; border narrow and extended into a curved spine.

Thorax and pygidium unknown.

Remarks.—The high relief of the cranidium caused by the deep dorsal and marginal furrows and elevated palpebral lobes is the distinguishing feature of this species. It occurs higher in the *Conaspis* zone than *Taenicephalus shumardi* (Hall).

Occurrence.—*Conaspis* zone, Franconia formation; Hudson, Wis., F-2.16, 2.17a; Marine, Minn., F-29.1; Copas, Minn., F-31.1.

Syntypes.—Cranidium, T6504a; cephalon, T6504b; free cheek, T6504c.

Genus WILBERNIA Walcott, 1924

WILBERNIA HALLI Resser

Plate 107, figures 17, 19

Conocephalites diadematus HALL (part), 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 167, pl. 7, figs. 37, 38.

Dicellocephalus misa BERKEY, 1898, Am. Geologist, vol. 21, p. 290, pl. 20, figs. 12, 13.

Wilbernia halli RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 28.

Remarks.—This species is characteristic of the *Conaspis* zone. It is characterized by a conspicuously tapered glabella and a brim-border ratio of 1:2.

Occurrence.—*Conaspis* zone, Franconia formation; Hudson, Wis., 2.17a; Nigger Coulee, Wis., F-3.28a; Marine, Minn., F-29.1; Copas, Minn., F-31.1; Franconia, Minn., F-16.12, 17.12, 17.15, 17.16, 17.20, 36.7, 36.8; Taylors Falls, Minn., F-18.13, 18.14, 18.15, 18.16, 24.7, 24.16, 24a.8.

Hypotypes.—Cranidium, T6576a; pygidium, T6576b, free cheek, T6576c.

WILBERNIA HALLI var. A

Plate 107, figures 9, 16

At two localities the *Wilbernia halli* population contains a few variants characterized by notable concavity of the frontal area and a brim-border ratio of 1:4 as compared with the convex frontal area and 1:2 ratio in the typical specimens. The pygidial border of this variant is also concave.

Occurrence.—*Conaspis* zone, Franconia formation; Franconia, Minn., F-16.12, 17.16.

Holotype.—Cranidium, T6577a; paratype, pygidium, T6577b.

PTYCHASPIS-PROSAUKIA ZONE

Genus EOPTYCHASPIS Nelson, n. gen.

Glabella cylindrical, highly convex, elevated above free cheeks, rounded anteriorly; downward anterior flexure of glabella begins at about mid-point; frontal area separated into brim and border by faint marginal furrow; palpebral lobes small, about on midline of glabella; glabellar and dorsal furrows well marked; surface granulose.

Genotype.—*Eoptychaspis cylindricus* Nelson, n. sp.

Remarks.—This genus is intermediate between *Conaspis* and *Ptychaspis*. The granulose surface, the wider and upsloping fixed cheeks, and the wider posterior limbs are

characters suggesting ptychaspid affinities while the brim and border are conaspid attributes.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation.

EOPTYCHASPIS CYLINDRICUS Nelson, n. sp.
Plate 108, figures 1–5

Glabella cylindrical, highly convex, straight sided to slightly tapered, rounded anteriorly, length greater than width; two pairs of glabellar furrows, posterior pair well impressed, oblique at sides and transverse across axis of glabella, anterior pair slightly oblique and not reaching axis; occipital furrow distinct; occipital ring narrow; dorsal furrow well impressed; frontal area less than one-fourth length of glabella, downsloping to nearly flat, made up of brim and border separated by marginal furrow; fixed cheeks upsloping, about one-fourth width of glabella; palpebral lobes small, lying about on midline of the glabella; posterior limbs wide, triangular, about same length as occipital ring.

Free cheeks, thorax and pygidium unknown.

Remarks.—This species shows variations in tapering and rounding of anterior part of glabella and in slope and size of the frontal area. The specimens show all gradations between extreme forms.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Marine, Minn., F-29.3, 29.5, 29.6; Copas, Minn., F-31.4.

Syntypes.—Cranidia, T6554a, T6554b, T6554c, T6554d, T6554e.

EOPTYCHASPIS CYLINDRICUS var. A
Plate 108, figures 8, 9

Remarks.—This variant is characterized by a bulbous anterior part of the glabella and a steeply downsloping brim and border. It is uncommon and known from only one locality.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Marine, Minn., F-29.5.

Holotype.—Cranidium, T6557a; Paratype, cranidium, T6557b.

Genus IDAHOIA Walcott, 1924
IDAHOIA HERA (Walcott)
Plate 109, figure 16

Saratogia hera WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 197, pl. 35, figs. 3, 3a–b.

Idahoia hera RESSER, 1935, Smithsonian Misc. Coll., vol. 93, no. 5, p. 36.

Remarks.—This species differs from *I. wisconsensis* (Owen) and *I. hamulus* (Owen), both of which occur higher in the *Ptychaspis-Prosaukia* zone elsewhere in the Upper Mississippi valley, in having wider fixed cheeks, a more tapering glabella, and a relatively wider brim than border. At Marine, the type locality of the species, it occurs low in the *Stigmacephalus oweni* subdivision.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.17; Nigger Coulee, Wis., F-3.28C; Arcola, Minn., F-15.1, 15.4; Marine, Minn., F-29.3, 29.5, 29.6.

Topotype.—Cranidium, T6587a.

Genus MONOCHEILUS Resser, 1937
MONOCHEILUS ANATINUM (Hall)
Plate 110, figure 15

Conocephalites anatinus HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 158, pl. 7, figs. 34, 35.
Conaspis anatina HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 152; WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357.
Ptychoparia anatina MILLER, 1889, North American geology and palaeontology, p. 565.
Monocheilus anatinus RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 20.
Monocheilus anatinum SHIMER & SHROCK, 1944, Index fossils of North America, p. 629, pl. 266, figs. 1–3.

Remarks.—*Monocheilus* resembles *Stigmacephalus* except that it has a shorter frontal area, the palpebral lobes are more than twice as large and the posterior limbs are narrower.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.19; Arcola, Minn., F-15.2; *Ptychaspis granulosa* faunule, Franconia formation; Hudson, Wis., F-2.21, 2.24; Arcola, Minn., F-15.6.

Hypotype.—Cranidium, T6572a.

Genus PROSAUKIA Ulrich & Resser, 1933
PROSAUKIA CURVICOSTATA Ulrich & Resser
Plate 110, figures 6, 16, 18

Prosaukia curvicostata ULRICH & RESSER, 1933, Milwaukee Public Mus. Bull., vol. 12, p. 145, pl. 25, figs. 1–7.

Remarks.—This species occurs in white and brown mottled, well-cemented sandstone similar to beds termed the Mazomanie

formation by Ulrich in central Wisconsin.

Occurrence.—*Prosaukia curvicostata* faunule, Franconia formation; Marine, Minn., F-28.11, 29.24; Stillwater, Minn., F-21.10.

Hypotypes.—Cranidium, T6589a; free cheek, T6589b; pygidium, T6589c.

Genus PTYCHASPIS Hall, 1863

PTYCHASPIS ARCOLENSIS Nelson, n. sp.

Plate 108, figures 6, 7

Glabella cylindrical, highly convex, slightly tapered and straight sided, rounded anteriorly, length nearly twice the width, slightly elevated above fixed cheeks; two pairs of glabellar furrows, posterior pair oblique, deeply impressed at sides, faint and transverse across glabellar axis, anterior pair faint, less oblique, not reaching axis; occipital furrow especially distinct at sides of glabella; occipital ring narrow; dorsal furrow well impressed; frontal area steeply downsloping, less than one-fourth length of glabella, no differentiation into brim and border; fixed cheeks upsloping, more than one-third width of glabella; palpebral lobes small, lying just posterior to midline of glabella; posterior limbs wide, triangular, slightly longer than occipital ring; surface pustulose.

Free cheek, thorax and pygidium unknown.

Remarks.—This species differs from *Ptychaspis granulosa* (Owen) in having the glabella slightly elevated above the fixed cheeks instead of on the same level; the anterior flexure of the glabella more gradual, beginning from just anterior to the midpoint; the frontal area steeply downsloping instead of vertical, and the more posterior position of the palpebral lobes.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.19; Arcola, Minn., F-15.1, 15.2, 15.3, 15.4.

Holotype.—Cranidium, T6556a; paratype, cranidium, T6556b.

PTYCHASPIS GRANULOSA (Owen)

Plate 110, figure 8

Dikelocephalus granulosus OWEN, 1852, Geol. Survey Wisconsin, Iowa, Minnesota Rept., p. 575, table 1, fig. 7.

not *Ptychaspis granulosa* HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 173, pl. 6, figs. 33–40.

Ptychaspis granulosa WHITFIELD, 1878, Geol. Survey Wisconsin Ann. Rept. 1877, p. 54; ——, 1882, Geology of Wisconsin, vol. 4, p. 185, pl. 1, fig. 24.

not *Ptychaspis granulosa* SHIMER & SHROCK, 1944, Index fossils of North America, p. 631, pl. 262, figs. 18–21.

Remarks.—The specimens figured by Hall and refigured by Shimer and Shrock belong to *P. striata* Whitfield.

Ptychaspis granulosa is characterized by having glabella and fixed cheeks on the same level, abrupt downturning of the anterior portion of the cranidium, and the vertical frontal area.

Occurrence.—*Ptychaspis granulosa* faunule, Franconia formation; Hudson, Wis., F-2.21, 2.24; Arcola, Minn., F-15.5, 15.6.

Hypotype.—Cranidium, T6588a.

PTYCHASPIS MINISCAENSIS (Owen)

Plate 110, figure 20

Dikelocephalus miniscaensis OWEN, 1852, Geol. Survey Wisconsin, Iowa, Minnesota Rept., p. 574, pl. 1, fig. 3a, pl. 1A, figs. 4, 5.

Ptychaspis miniscaensis HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 171, pl. 6, figs. 41–45, pl. 10, figs. 21, 22; RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 449; SHIMER & SHROCK, 1944, Index fossils of North America, p. 631, pl. 262, fig. 1.

Remarks.—This species, although represented only by poorly preserved specimens, can be distinguished from others by the somewhat less convex cranidium, and the wide smooth posterior limbs.

Occurrence.—*Ptychaspis miniscaensis* faunule, Franconia formation; Afton, Minn., F-35.1; Hudson, Wis., F-2.31; Arcola, Minn., F-15.11; Copas, Minn., F-31.11.

Hypotype.—Cranidium, T6580a.

Genus STIGMACEPHALUS Resser, 1937

Stigmacephalus RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 25.

Remarks.—In establishing this genus, Resser included only two species: *Conocephalites oweni* Hall, the genotype, and *Arionellus bipunctatus* Shumard. These two do not seem to be congeneric. *C. oweni* does not possess "pits in the anterior angles of the dorsal furrows," nor does it generally possess "a faint anterior furrow" as described by Resser. These features, therefore, are not generic characters of *Stigmacephalus*.

Stigmacephalus differs from *Croixana* in possessing an expanding arcuate frontal area as compared with the pronounced ta-

pering in the latter, narrower fixed cheeks, larger and less curved palpebral lobes which lie about on the midline of the glabella instead of anteriorly as in *Croixana*, and the absence of anterior pits.

Stigmacephalus resembles *Monocheilus*, except that the latter has distinctly larger eyes and a narrower frontal area.

Occurrence.—Stigmacephalus oweni faunule, Franconia formation.

Genotype.—Conocephalites oweni Hall 1863.

STIGMACEPHALUS OWENI (Hall)
Plate 109, figures 1, 2, 9, 14, 15

Conocephalites oweni HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 155, pl. 8, figs. 17, 20.
Conaspis oweni HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 152; WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357.
Ptychoparia oweni MILLER, 1889, North American geology and palaeontology, p. 565.
Stigmacephalus oweni RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 26 (designated by Resser as genotype of *Stigmacephalus*).

Remarks.—This is the most common species of the *Stigmacephalus oweni* faunule. The convex glabella and its rounded anterior margin are its distinguishing features. Mature forms have less rounded anterior margins and generally show faint glabellar furrows. The species is especially abundant at Marine, Minnesota, the type locality.

Occurrence.—Stigmacephalus oweni faunule, Franconia formation; Hudson, Wis., F-2.17, 2.19; Nigger Coulee, Wis., F-3.28c; Arcola, Minn., F-15.1, 15.4; Marine, Minn., F-29.3, 29.5, 29.6; Copas, Minn., F-31.4.

Topotypes.—Cranidia, T6561a, T6561b, T6561c, pygidium, T6561d; hypotype, cranidium, T6586a.

STIGMACEPHALUS OWENI var. A
Plate 109, figures 3–7

Glabella convex, tapered, anterior margin straight with rounded corners, length equal to width; two pairs of very faint oblique glabellar furrows; occipital furrow faint; occipital ring about one-fourth length of glabella; dorsal furrow moderate; frontal area slightly convex and downsloping, slightly tapered to slightly expanded anteriorly, somewhat pointed to smoothly arcuate anterior margin, over one-third length of glabella; fixed cheeks very narrow, about one-sixth width of glabella; palpebral lobes between one-third and one-half length of glabella, lying about on midline of glabella; posterior limbs of medium width, shorter than occipital ring.

Free cheeks, thorax and pygidium unknown.

Remarks.—The *S. oweni* population includes two distinct variants of which this is the more abundant. It differs from typical specimens in possessing a more tapered glabella, the variable shape, from pointed to smoothly arcuate, of the frontal area, and generally more slender posterior limbs.

Occurrence.—Stigmacephalus oweni faunule, Franconia formation; Hudson, Wis., F-2.18; Arcola, Minn., F-15.1, 15.3, 15.4; Copas, Minn., F-31.4, 31.6.

Holotype.—Cranidium, T6559a; paratypes, cranidia, T6559b, T6560a, T6560b, T6560c.

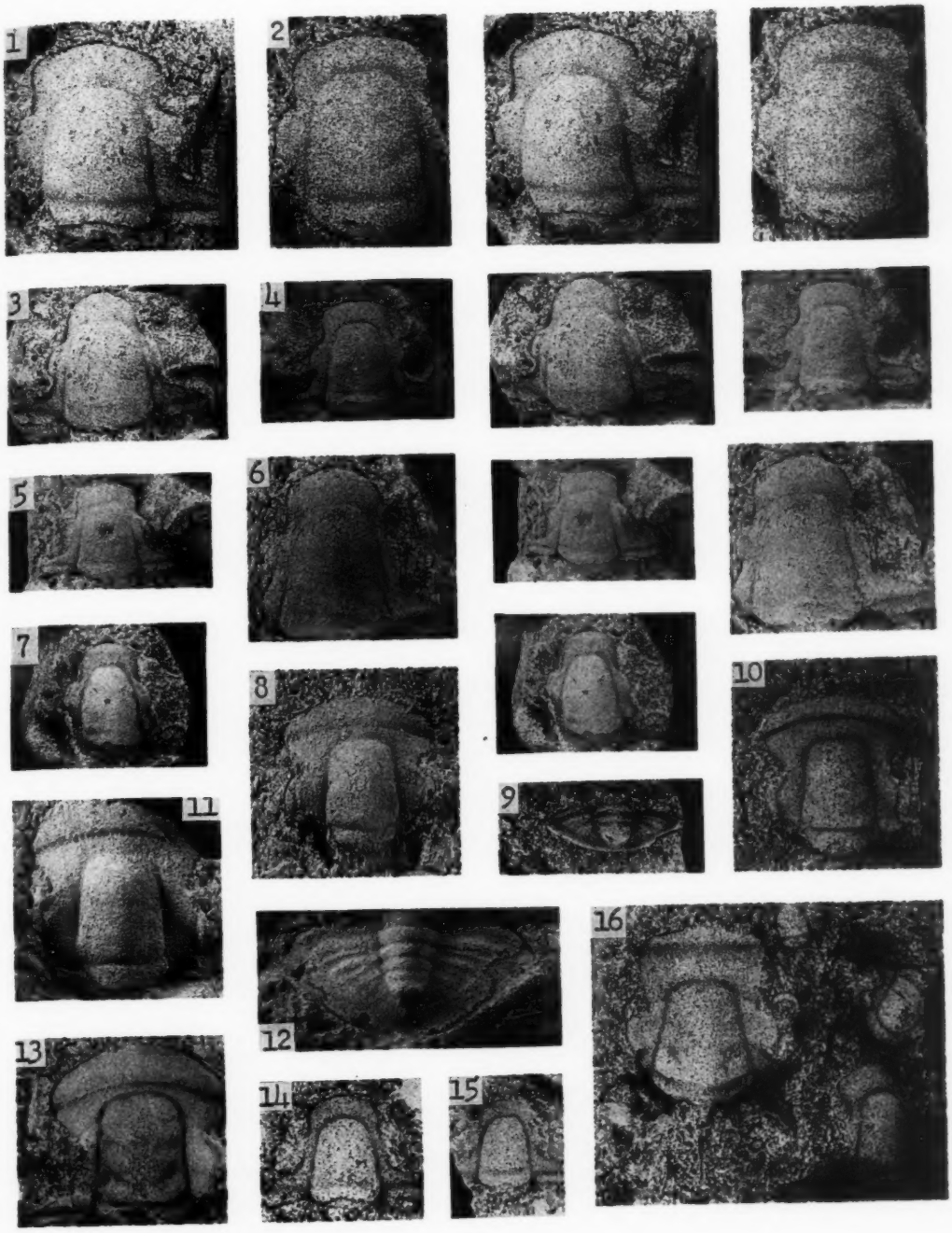
STIGMACEPHALUS OWENI var. B
Plate 108, figures 10, 11

Glabella convex, tapered, anterior margin straight but rounded at corners, length equal to width; two pairs of faint oblique glabellar furrows; occipital furrow faint;

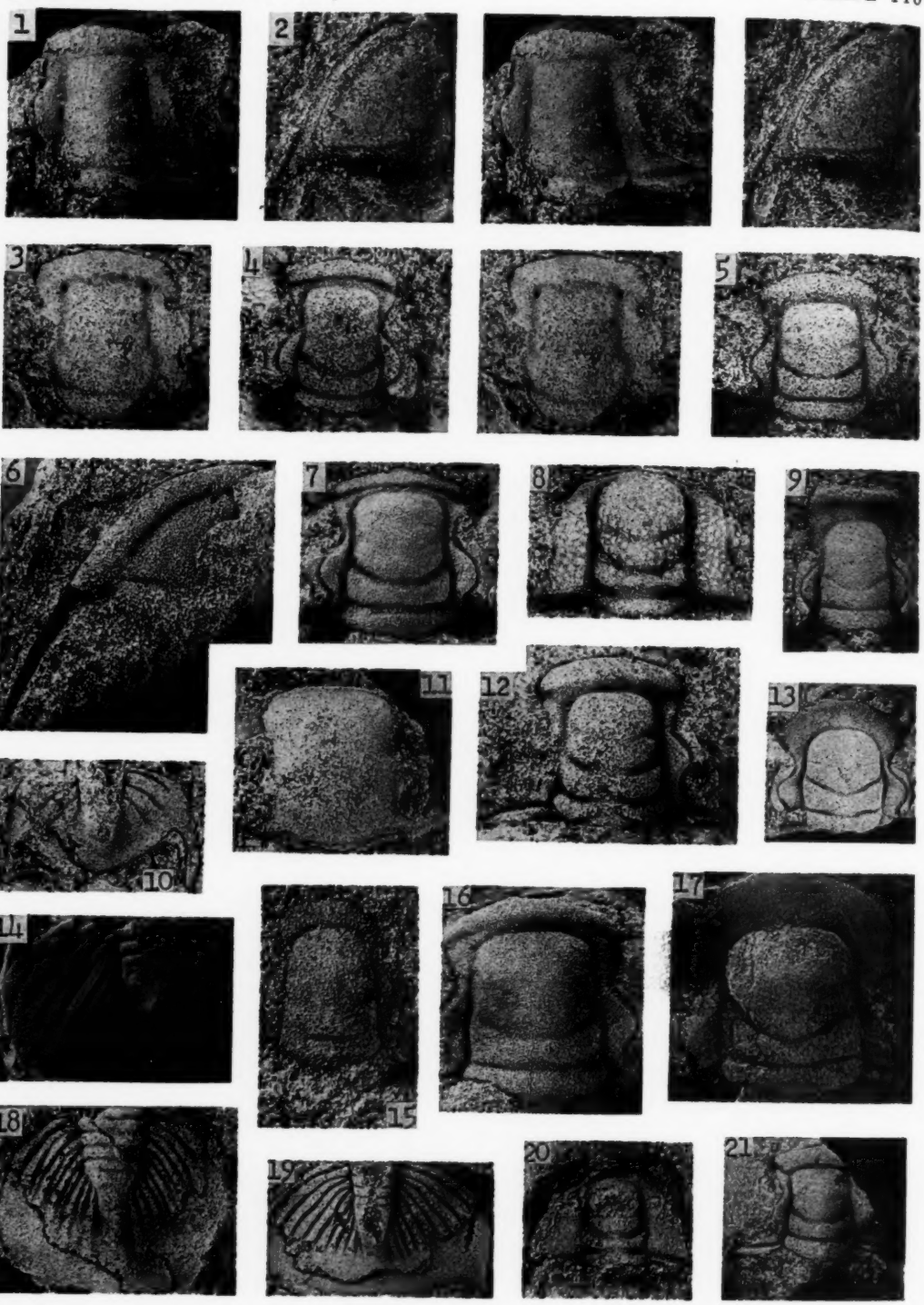
EXPLANATION OF PLATE 109

Ptychaspis-Prosaukia zone
Stigmacephalus oweni faunule—Franconia formation
(Figures *1–7* in stereographic pairs)

FIGS. *1, 2, 9, 14, 15—Stigmacephalus oweni* (Hall). Topotypes: *1*, cranidium, ×2, T6561a, F-29.5; *2*, cranidium, ×2, T6561b, F-29.5; *9*, pygidium, ×2, T6561d, F-29.6; *14*, cranidium, ×2, T6561c, F-29.6. *15*, Hypotype; cranidium, ×2, T6586a, F-3.28C. (p. 780)
3–7—Stigmacephalus oweni, var. A. *3*, Paratype; cranidium, ×1.5, T6560b, F-15.4. *4*, Holotype; cranidium, ×1, T6559a, F-2.18. *5*, Paratype; cranidium, ×1, T6559b, F-2.18. *6*, Paratype; cranidium, ×1.5, T6560c, F-15.1. *7*, Paratype; cranidium, ×1, T6560a, F-15.4. (p. 780)
8, 11, 12—Wilbernia diademata (Hall). *8*, Hypotype; cranidium, ×1.5, T6583a, F-31.4. *11*, Hall's type cranidium, ×1.5, AMNH 314/1, F-29.3. *12*, Hall's type pygidium, ×1.5, AMNH 314/1, F-29.3. (p. 782)
10—Wilbernia explanata (Whitfield). Hypotype; cranidium, ×1.5, T6582a, F-15.1. (p. 782)
13—Wilbernia pero (Walcott). Hypotype; cranidium, ×1, T6584a, F-2.18. (p. 782)
16—Idahoia hera (Walcott). Topotype; cranidium, with three cranidia of *Stigmacephalus oweni* (Hall), ×2, T6587a, F-29.6. (p. 778)



Nelson, Cambrian trilobites



Nelson, Cambrian trilobites

occipital ring less than one-fourth length of glabella; dorsal furrow moderate; brim convex, downsloping, expanding anteriorly, making up three-fourths of frontal area; faint marginal furrow separates brim from border, having smooth arcuate margin; frontal area just less than one-third length of glabella, width slightly greater than maximum width of glabella; fixed cheeks flat, about one-fifth width of glabella; palpebral lobes upsloping, one-third length of glabella, lying just anterior to midline of glabella; posterior limbs wide, shorter than occipital ring.

Free cheeks, thorax and pygidium unknown.

Remarks.—This member of the *S. oweni* population is rare, occurring at only two localities. The marginal furrow, marked anterior expansion of brim, and wide posterior limbs are characteristic.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Nigger Coulee, Wis., F-3.28B; Marine, Minn., F-29.3.

Holotype.—Cranidium, T6558a; paratype, cranidium, T6558b.

Genus STIGMASPIS Nelson, n. gen.

Cranidium with large, rectangular, slightly tapered glabella, bearing pits at anterior corners of moderate dorsal furrow; brim triangular, only present in front of fixed cheeks; border short, having smooth, arcuate anterior margin; marginal furrow faint, leading from anterior corners of dorsal furrow to anterior corners of border; palpebral lobes one-third to one-fourth of glabella; fixed cheeks about one-fourth width of glabella; posterior limbs of medium width.

Remarks.—This genus shows some resemblances to certain members of the *Saukia* fauna, especially to *Tellerina*, which have been reported from the same zone. *Stigmaspis* differs in the following respects: it lacks the anterior expansion of the glabella, so common in the *Saukia* group, the glabellar furrows are very faint in *Stigmaspis*, and it has wide, triangular posterior limbs.

Genotype.—*Stigmaspis hudsonensis* Nelson, n. sp.

Occurrence.—*Ptychaspis miniscaensis* faunule, Franconia formation.

STIGMASPIS HUDSONENSIS Nelson, n. sp.
Plate 110, figures 1–3

Glabella convex, rectangular in outline, slightly tapered, length slightly greater than width; two pairs of oblique glabellar furrows, anterior pair faint; occipital furrow moderate; occipital ring about one-fifth length of

EXPLANATION OF PLATE 110

(Figures *1–3* in stereographic pairs)

FIGS. *1–3*—*Stigmaspis hudsonensis* Nelson, n. gen., n. sp. *1*, Paratype; cranidium, ×1.5, T6563b, F-2.31. *2*, Paratype; free cheek, ×1.5, T6563c. *3*, Holotype; cranidium, ×1, T6563a, F-2.31. *Ptychaspis miniscaensis* faunule, Franconia formation. (p. 781)

4, 7—*Saukiella pyrene* (Walcott). *4*, Topotype; cranidium, ×2, T6600a, F-37a.4. *7*, Hypotype, cranidium, ×2, T6601a, F-28.14. *Osceolia* fauna, Jordan formation. (p. 783)

5, 12—*Tellerina leucosia* (Walcott). *5*, Topotype; cranidium, ×3, T6603a, F-37.12. *12*, Topotype; cranidium, ×2, T6602a, F-37a.4. *Osceolia* fauna, Jordan formation. (p. 783)

6, 16, 18—*Prosaukia curvicostata* Ulrich & Resser. *6*, Hypotype; free cheek, ×1.5, T6589b, F-28.11. *16*, Hypotype; cranidium, ×1.5, T6589a, F-28.11. *18*, Hypotype; pygidium, ×1, T6589c, F-28.11. *Prosaukia curvicostata* faunule, Franconia formation. (p. 778)

8—*Ptychaspis granulosa* (Owen). Hypotype; cranidium, ×2, T6588a, F-2.24. *Ptychaspis granulosa* faunule, Franconia formation. (p. 779)

9, 10—*Osceolia osceola* (Hall). *9*, Topotype; cranidium, ×2, T6604a, F-37a.4. *10*, Topotype; pygidium, ×1.5, T6604b, F-37a.4. *Osceolia* fauna, Jordan formation. (p. 783)

11—*Illaenurus quadratus* Hall. Topotype; cranidium, ×2, T6607a, F-37.12, *Osceolia* fauna, Jordan formation. (p. 783)

13, 19—*Dikelocephalus thwaitesi* Ulrich & Resser. *13*, Hypotype; cranidium, ×1.5, T6605a, F-28.14. *19*, Topotype; pygidium, ×1, T6606a, F-37a.4. *Osceolia* fauna, Jordan formation. (p. 783)

14, 17—*Dikelocephalus minnesotensis* Owen. *14*, Topotype; pygidium, ×1, T6595a, F-21.14. *17*, Topotype; cranidium, ×1, T6594a, F-22.3. Upper *Dikelocephalus* zone, Lodi silt, St. Lawrence formation. (p. 784)

15—*Monocheilus anatinum* (Hall). Hypotype; cranidium, ×3, T6572a, F-2.21. *Ptychaspis granulosa* faunule, Franconia formation. (p. 778)

20—*Ptychaspis miniscaensis* (Owen). Hypotype; cranidium, ×1, T6580a, F-31.11, *Ptychaspis miniscaensis* faunule, Franconia formation. (p. 779)

21—*Calvinella wisconsinensis* Ulrich & Resser. Hypotype; cranidium, ×1, T6599a, F-35a.1. Upper *Dikelocephalus* zone, Lodi silt, St. Lawrence formation. (p. 784)

glabella; dorsal furrow moderate, bearing faint to well impressed pits at anterior corners of glabella; brim triangular, small; border convex, downsloping, about one-fourth length of glabella; faint marginal furrow leading from anterior pits to outer corners of cranidium; fixed cheeks upsloping, about one-fourth width of glabella; palpebral lobes one-third to one-fourth length of glabella; posterior limbs of medium width, length less that that of occipital ring.

Free cheeks convex, flat near eyes; marginal furrow shallow; border narrow; long curved spine present.

Thorax and pygidium unknown.

Remarks.—This species is rare in this area and the only member of the genus so far discovered. It is characterized by the anterior pits and the rectangular, slightly tapering glabella.

Occurrence.—*Ptychaspis miniscaensis* faunule, Franconia formation; Hudson, Wis., F-2.31.

Holotype.—Cranidium, T6563a; paratypes, cranidium, T6563b, free cheek, T6563c.

Genus WILBERNIA Walcott, 1924

WILBERNIA DIADEMATA (Hall)

Plate 109, figures 8, 11, 12

Conocephalites diadematus HALL (part), 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 167, pl. 7, fig. 36, pl. 8, fig. 21 (not pl. 7, figs. 37, 38, pl. 8, fig. 18).

not *Ptychoparia (?) diadematus* WALCOTT, 1899, U. S. Geol. Survey Mon. 32, p. 462, pl. 64, figs. 2–2c.

Wilbernia diadematus RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 28.

Remarks.—This can be distinguished from other species of *Wilbernia* in the *Ptychaspis-Prosaukia* zone by the ratio of brim and border widths, 1:2, against 1:1 in *W. explanata* and approximately 1:5 in *W. pero*. *W. diadematus* can be distinguished from *W. halli* of the *Conaspis* zone, which also has a brim-border ratio of 1:2, by the straight sided, only slightly tapered glabella instead of the conspicuously tapering glabella of *W. halli*. At Marine, the type locality, it occurs with abundant specimens of *Stigmacephalus oweni*.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Arcola Minn., F-15.1; Marine, Minn., F-29.3, 29.5, 29.6; Copas, Minn., F-31.4.

Holotype.—Cranidium, AMNH 314/1; paratype, pygidium, AMNH 314/1; hypotype, cranidium, T6583a.

WILBERNIA EXPLANATA (Whitfield)

Plate 109, figure 10

Conocephalites (Ptychaspis) explanatus WHITFIELD, 1880, Wisconsin Geol. Survey Ann. Rept. 1879, p. 49; ——, 1882, Geology of Wisconsin, vol. 4, p. 181, pl. 1, figs. 27, 28.

Ptychoparia explanata MILLER, 1889, North American geology and palaeontology, p. 565.

Wilbernia explanata TWENHOFEL, RAASCH & THWAITES, 1935, Geol. Soc. America Bull., vol. 46, p. 1742; RAASCH, 1939, idem, Special Paper 19, p. 97; LOCHMAN, 1950, Jour. Paleontology, vol. 24, p. 330, pl. 46, figs. 15–17.

Idahoia explanata RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 14.

Wilbernia hudsonensis RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 28.

Remarks.—This species is characterized by a brim-border ratio of 1:1. *Wilbernia hudsonensis* Resser is included in the synonymy after examination of the types of both species which were described from the same type locality at Hudson, Wisconsin. Whitfield described only the cranidium and Resser only the pygidium.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.18, 2.19; Arcola, Minn., F-15.1; Marine, Minn., F-29.6. *Ptychaspis granulosa* subzone, Franconia formation; Arcola, Minn., F-15.6.

Hypotype.—Cranidium, T6582a.

WILBERNIA PERO (Walcott)

Plate 109, figure 13

Ptychoparia pero WALCOTT, 1890, U. S. Nat. Mus. Proc., vol. 13, p. 274, pl. 21, fig. 6.

Anomocare pero WALCOTT, 1912, U. S. Geol. Survey Mon. 51, p. 212.

Wilbernia pero WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 60, pl. 13, fig. 4; Frederickson, 1949, Jour. Paleontology, vol. 23, p. 362, pl. 72, figs. 7–9 (for synonymy to date).

Remarks.—This species is characterized by a narrow brim and a wide convex border, the ratio being approximately 1:5.

Occurrence.—*Stigmacephalus oweni* faunule, Franconia formation; Hudson, Wis., F-2.17, 2.18; Nigger Coulee, Wis., F-3.28c; Marine, Minn., F-29.3.

Hypotype.—Cranidium, T6584a.

OSCEOLIA FAUNA

Genus DIKELOCEPHALUS Owen, 1852

DIKELOCEPHALUS THWAITESI Ulrich & Resser

Plate 110, figures 13, 19

Dikelocephalus thwaitesi ULRICH & RESSER, 1930, Milwaukee Public Mus. Bull., vol. 12, p. 54, pl. 21, figs. 1–10 (for synonymy to date).

Remarks.—This species is characterized by the arcuate concave frontal area. The pronounced thickening of the border, mentioned by Ulrich and Resser as characteristic, is not present in the specimens in the collections. The species is common in the Jordan sandstone at Osceola, the type locality.

Occurrence.—*Osceolia* fauna, basal Jordan formation; Marine, Minn., F-28.14; Osceola, Wis., F-37.12; Osceola bridge section, Minn., F-37a.4.

Topotype.—Pygidium, T6606a; hypotype, cranidium, T6605a.

Genus ILLAENURUS Hall, 1863

ILLAENURUS QUADRATUS Hall

Plate 110, figure 11

Illaenurus quadratus HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 176, pl. 7, figs. 52–57; WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 5, p. 406, pl. 45, figs. 1, 1a–e (for synonymy to date); ——, 1924, idem, vol. 75, no. 2, pl. 14, fig. 7; WALTER, 1924, Iowa Geol. Survey Ann. Repts. 1923, 1924, vol. 31, p. 189; SHIMER & SHROCK, 1944, Index fossils of North America, p. 627, pl. 260, figs. 16–19.

Remarks.—This species is found in both the St. Lawrence and Jordan formations at Osceola, the type locality for the species. *I. calvini* Walter, which apparently is restricted to the St. Lawrence (Lodi silts), is the only other member of the genus known in this area.

Occurrence.—*Osceolia* fauna, St. Lawrence formation; Osceola, Wis., F-37.10. *Osceolia* fauna, basal Jordan formation; Marine, Minn., F-28.14; Osceola, Wis., F-38.12; Osceola bridge section, Minn., F-37a.4.

Topotype.—Cranidium, T6607a.

Genus OSCEOLIA Walcott, 1914

OSCEOLIA OSCEOLA (Hall)

Plate 110, figures 9, 10

Dikelocephalus osceola HALL, 1863, New York State Cab. Nat. History 16th Ann. Rept., p. 146, pl. 10, figs. 18, 19; pl. 7, fig. 49.

Osceolia osceola ULRICH & RESSER, 1930, Milwaukee Public Mus. Bull., vol. 12, p. 69, pl. 22, figs. 1–9 (for synonymy to date); SHIMER & SHROCK, 1944, Index fossils of North America, p. 629, pl. 262, figs. 9, 10.

Remarks.—This species is characterized by the sharply upturned anterior margin of the frontal area and the long curved lateral spines on the pygidium.

Occurrence.—*Osceolia* fauna, St. Lawrence formation (Lodi); Osceola, Wis., F-37.10. Basal Jordan formation; Osceola, Wis., F-37.12; Osceola bridge section, Minn., F-37a.4.

Topotypes.—Cranidium, T6604a; pygidium, T6604b.

Genus SAUKIELLA Ulrich and Resser, 1933

SAUKIELLA PYRENE Walcott

Plate 110, figures 4, 7

Saukia pyrene WALCOTT, 1913, Smithsonian Misc. Coll., vol. 57, no. 13, p. 382, pl. 67, figs. 18–20.

Saukiella pyrene ULRICH & RESSER, 1933, Milwaukee Public Mus. Bull., vol. 12, p. 204, pl. 34, pl. 35, figs. 1–11.

Remarks.—This species is common at Osceola, the type locality, and it is a good marker for this fauna. It is characterized by the slender glabella with only the posterior glabellar furrow generally visible, and the triangular border.

Occurrence.—*Osceolia* fauna, basal Jordan formation; Marine, Minn., F-28.14; Osceola, Wis., F-37.12; Osceola bridge section, Minn., F-37a.4.

Topotype.—Cranidium, T6600a; hypotype, cranidium, T6601a.

Genus TELLERINA Ulrich & Resser, 1933

TELLERINA LEUCOSIA (Walcott)

Plate 110, figures 5, 12

Saukia leucosia WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 379, pl. 67, figs. 14–17a.

Tellerina? leucosia ULRICH & RESSER, 1933, Milwaukee Public Mus. Bull., vol. 12, p. 257, pl. 44, figs. 1–11, 18–20.

Remarks.—This species is characterized by the smooth tapering of the glabella, the convexity of the border, and the absence of brim in front of the glabella. It is common at Osceola, the type locality.

Occurrence.—*Osceolia* fauna, basal Jordan formation; Stillwater, Minn., F-21.19; Marine, Minn., F-28.14; Osceola, Wis., F-37.12;

Osceola bridge section, Minn., F-37a.4; *Osceolia* fauna, St. Lawrence formation (Lodi), Osceola, Wis., F-37.10.

Topotypes.—Cranidia, T6603a, T6602a.

UPPER DIKELOCEPHALUS ZONE

Genus CALVINELLA Walcott, 1914

CALVINELLA WISCONSINENSIS

Ulrich & Resser

Plate 110, figure 21

Calvinella wisconsinensis ULRICH & RESSER, 1933, Milwaukee Public Mus. Bull., vol. 12, p. 240, pl. 40, figs. 23–33.

Remarks.—*Calvinella* resembles *Tellerina* except for the possession of an occipital spine. This species is characterized by the deep impression and oblique position of the marginal furrow at the sides of the cranidium.

Occurrence.—Upper *Dikelocephalus* zone, St Lawrence formation (Lodi silts); Afton, Minn., F-35a.1.

Hypotype.—Cranidium, T6599a.

Genus DIKELOCEPHALUS Owen, 1852

DIKELOCEPHALUS MINNESOTENSIS Owen

Plate 110, figures 14, 17

Dikelocephalus minnesotensis OWEN, 1852, Geol. Survey Wisconsin, Iowa and Minnesota Rept., p. 574, table 1, figs. 1, 2, table 1a, figs. 3, 6; WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 369, pl. 60, figs. 1–8, pl. 61, figs. 1–3, 5–7, pl. 66, fig. 1 (for synonymy to date); ULRICH & RESSER, 1930, Milwaukee Public Mus. Bull., vol. 12, p. 20, pl. 1, figs. 6–8, pl. 3, fig. 1; SHIMER & SHROCK, 1944, Index fossils of North America, p. 623, pl. 261, figs. 7, 8.

Remarks.—Many specimens have been assigned to this species in the past and restriction of the species to little more than the original material of Owen by Ulrich and Resser appears to be of doubtful value. Specimens from the St. Croix valley are not abundant and it seems best to refer all of them to this species whose types came from Stillwater.

Occurrence.—Upper *Dikelocephalus* zone, St. Lawrence formation (Lodi silts); Afton, Minn., F-35.11; Stillwater, Minn., F-21.14, 22.3.

Topotypes.—Cranidium, T6594a; pygidium, T6595a.

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CONODONTS FROM THE LOWER MISSISSIPPIAN WASSONVILLE DOLOMITE OF IOWA

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ABSTRACT—A sparse conodont collection has been secured from a shaly portion of the Wassonville dolomite in southeastern Iowa. The assemblage as a whole is none too well preserved, but a number of complete or essentially complete conodonts have been obtained. The described specimens include representatives of the genera *Hibbardella, Hindeodella, Ligonodina, Polygnathus, Prioniodus, Siphonodella, Solenodella,* and *Spathognathodus*. Unfigured fragmentary specimens in the collection indicate that the genera *Euprioniodina, Lonchodina,* and *Ozarkodina* are also present in the fauna. This assemblage indicates late Kinderhook age and suggests close relationship to the English River and Prospect Hill sandstone faunas of Iowa and to Bushberg and Hannibal faunas in Missouri.

INTRODUCTION

ALTHOUGH most Lower Mississippian rocks of Iowa have been studied rather extensively, the Wassonville dolomite, named by Bain (1895, p. 322), appears to have been treated only briefly. Relatively the most important study is that by Laudon (1931, pp. 371–383), and we have drawn freely from it for aid in the preparation of the present report.

The Wassonville, in its type area at least, is a rather well defined stratigraphic unit. It attains a maximum thickness of about 40 to 45 feet, but is commonly somewhat less and thicknesses at adjacent localities may differ appreciably. Bain termed this stratigraphic unit a limestone, but most of the Wassonville is brown dolomite with numerous stringers and nodules of white chert.

The type section of the Wassonville is near the old Wassonville Mill along the south bank of English River in Washington County, Iowa. The Wassonville is well exposed in one or two adjacent counties but the best outcrops are along the valley of English River near the type area. All conodonts of the present study were obtained in 1948 from a locality described in detail by Laudon (1931, pp. 375, 383). This outcrop is in the NW¼ NW¼ sec. 19, T. 77 N., R. 7 W., Washington County, Iowa, along the south bluff of English River just southeast of the highway bridge.

The section (from Laudon, 1931, p. 383) is as follows:

	Feet
Wassonville	
4. Dolomite, brown, fractured, containing one chert band, fossiliferous, basal part containing much reworked English River grit	5
3. Shale, blue to gray, soft, unctuous, carrying chunks of English River grit. Numerous fish teeth in base	6
English River	
2. Gritstone, blue to gray, massive, very fossiliferous	5
Maple Mill	
1. Shale, deep blue to gray, very soft, unctuous, carbonaceous and stained at top, filled with pyrite in lower part, unfossiliferous	14

The conodonts came from the middle and upper portions of the 6-foot shale unit (no. 3) at the base of the Wassonville. The dolomite above contains no shale and did not yield conodonts. The Wassonville was also sampled at the Amana locality in Iowa County (Laudon, 1931, p. 377) but there it is entirely dolomite and no conodonts were secured.

Condonts are only moderately abundant at the Washington County locality. The assemblage, however, shows considerable variety and at least 11 genera are represented. The described fauna consists of the following forms:

Hibbardella sp.
Hindeodella aff. *echinata* E. R. Branson
Hindeodella sp.
Ligonodina sp.
Polygnathus communis Branson & Mehl
P. inornata E. R. Branson
P. sagittaria Youngquist & Patterson
P. aff. *symmetrica* E. R. Branson
Prioniodus barbatus Branson & Mehl
Siphonodella duplicata (Branson & Mehl)

S. quadruplicata (Branson & Mehl)
Solenodella tenera (E. R. Branson)?
Spathognathodus macer (Branson & Mehl)

To this list may be added fragmentary and unfigured representatives of *Euprioniodina*, *Lonchodina* and *Ozarkodina*. Fish spines and plates are common in the washed shale residue.

The Wassonville has been assigned either to the Kinderhook or to the Osage series. Bain in 1895 originally regarded it as the top of the Kinderhook. In 1928 it was considered equivalent to the Fern Glen by Moore and it was referred to the Osage in the classification adopted by Wilmarth (1938, p. 2282). Laudon, (1931, p. 382), however, stated that the "Wassonville fauna is very definitely a later Kinderhook fauna."

The Wassonville conodont assemblage indicates a close relationship to the Prospect Hill and English River sandstone faunas of Iowa and to Bushberg and Hannibal faunas in Missouri. Recently Mehl and Thomas (1947) published a study of conodonts from the Fern Glen of Missouri. Neither the Fern Glen nor the Wassonville conodont assemblage is large, but a comparison suggests that the Wassonville fauna is slightly but distinctly older than the Fern Glen. The current correlation chart of the Mississippian system of North American (Weller et al., 1948) places the Wassonville in the late Kinderhook immediately above the Prospect Hill sandstone, and somewhat below the Fern Glen formation. These relationships seem entirely logical from the evidence of the conodont collection. However, one factor regarding the shale containing these fossils should be clearly stated. In his 1931 report Laudon noted that the shale "carries the characteristic Wassonville fish fauna in its base," but added that the shale itself is probably reworked Maple Mill and English River material. In personal correspondence with the writers Laudon has further pointed out that there is an intermingling of English River and Wassonville species in the reworked beds.

The conodont collection consists of more than 100 specimens. They were secured primarily from the upper portion of the shale and some may have been reworked from older beds, but presumably others lived during Wassonville time. If there was intermingling of faunas, however, we have not been able to detect it, for there is not a single element in the collection which is now known to be distinctly limited to rocks younger than the Prospect Hill and English River. In addition, we find no trace of any of the several elements which appear to be characteristic of the Maple Mill. We believe that the Wassonville is closely related in time to the English River and Prospect Hill strata and therefore the conodonts of the Wassonville should not differ materially from those of the subjacent beds.

Professor L. R. Laudon has generously contributed a number of helpful suggestions regarding the stratigraphy and paleontology of the Lower Mississippian of Iowa in general and, in particular, the problems concerning the Wassonville. Professor A. K. Miller has likewise given of his time and advice. We express our appreciation for the use of research facilities and for secretarial aid received from the University of Idaho and the State University of Iowa in connection with this study. Mr. Howard Webster of Iowa City retouched the photographs. All type and figured specimens have been placed in the repository of the Geology Department at the State University of Iowa.

SYSTEMATIC PALEONTOLOGY

HIBBARDELLA sp.

Plate 111, figures 12, 13

Because of the prominent three-dimensional growth of *Hibbardella*, complete specimens are rare in most conodont collections. The genus is fairly common in the Wassonville. We illustrate two of the more nearly complete individuals, but they cannot be specifically identified with certainty. However, they are similar to forms described by Thomas from English River and Prospect Hill strata.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimens.—State Univ. Iowa 4187 (fig. 12), 4188 (fig. 13).

HINDEODELLA aff. ECHINATA E. R. Branson

Plate 111, figure 15

Bar compressed laterally and bears a moderately sharp keel aborally. Denticles

in an alternating series with one or two smaller ones between adjacent larger denticles. Denticles incline strongly posteriad, somewhat compressed, become progressively larger posteriorly. Cusp stout, subquadrangular in cross-section. Figured specimen incomplete at both extremities. Its fragmentary nature precludes specific identification, but this individual appears to be close to such forms as *H. echinata* E. R. Branson, described from the Hannibal formation of Missouri.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimen.—State Univ. Iowa 4189.

HINDEODELLA sp.
Plate 111, figure 14

Bar blade-like, thin, high, gently bowed and arched. Cusp small, cusp and denticles inclined posteriad. Denticles numerous, closely appressed but rounded; larger denticles alternate in position with one to three smaller ones. Germ denticles numerous. No closely similar forms seem to be known from strata of comparable age except possibly one or two of the specimens described by Cooper (Cooper and Sloss, 1943) from a shale in Montana and Alberta ascribed to the early Mississippian.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimen.—State Univ. Iowa 4190.

LIGONODINA, sp.
Plate 111, figure 16

Bar stout, moderately keeled. Denticles all incline strongly posteriad, irregularly spaced and sized. Cusp strongly recurved, sharpened on both sides, more strongly so posteriorly. Anticusp fractured on figured specimen, only a single small denticle preserved. This specimen resembles other early Mississippian forms such as *Lingonodina* sp. Branson & Mehl from the Chouteau, and *L.* sp. Branson & Mehl from the Bushberg, both in Missouri.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimen.—State Univ. Iowa 4191.

POLYGNATHUS COMMUNIS Branson & Mehl
Plate 111, figures 4, 5, 19, 20

Polygnathus communis E. B. BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, p. 293, pl. 24, figs. 1–4; E. R. BRANSON, 1934 [1933], idem, vol. 8, no. 4, p. 308, pl. 25, figs. 5, 6; E. B. BRANSON, 1938, idem, vol. 13, no. 3, p. 182; ——, et al., 1938, idem, vol. 13, no. 4, pp. 132, 145, pl. 33, fig. 55, pl. 34, figs. 39–41; COOPER, 1938, Jour. Paleontology, vol. 13, pp. 399, 420, pl. 39, figs. 1, 2, 9, 10, 23, 24; HASS, 1943, idem, vol. 17, p. 308; E. B. BRANSON & MEHL, in Shimer and Shrock, 1944, Index fossils of North America, p. 245, pl. 94, figs. 29–31; E. B. BRANSON, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 221, pl. 32, fig. 55; pl. 39, fig. 40; HASS, 1947, Jour. Paleontology, vol. 21, pp. 136, 137; MEHL & THOMAS, 1947, Denison Univ. Bull., Jour. Sci. Labs., vol. 40, pp. 7, 15, pl. 1, fig. 37; YOUNGQUIST & PATTERSON, 1949, Jour. Paleontology, vol. 23, p. 62, pl. 15, figs. 7, 8; THOMAS, 1949, Geol. Soc. America Bull., vol. 60, p. 411, pl. 3, fig. 37.

Polygnathus aff. *communis* KNECHTEL & HASS, 1938, Jour. Paleontology, vol. 12, p. 519.

Specimens very gently arched, more prominently bowed. Platform thick relative to blade, concave orally but essentially smooth except for nodose carina. The bowed specimen shown in figures 4 and 5 appears to resemble *P. communis* described by E. R. Branson (1934, pl. 25, fig. 5) from the Hannibal of Missouri. That shown in figures 19 and 20 is similar to the Prospect Hill form illustrated by Youngquist and Patterson's figures 7 and 8 on their plate 15.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also reported from the English River and Prospect Hill sandstones of the same State; strata of Bushberg, Hannibal, Chouteau, and Fern Glen age in Missouri; the basal Orangeville and basal Sunbury shales of Ohio; a "Bushberg-Hannibal horizon" in Oklahoma; and from a thin shale (Kinderhook) at the base of the Lodgepole limestone, Little Rocky Mountains, Montana.

Figured specimens.—State Univ. Iowa 4192 (figs. 4, 5), 4193 (figs. 19, 20).

POLYGNATHUS INORNATA E. R. Branson
Plate 111, figures 11, 17, 18

Polygnathus inornata E. B. BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, p. 293, pl. 24, figs. 5–7, specific name as-

cribed to E. R. BRANSON; E. R. BRANSON, 1934 [1933], idem, vol. 8, no. 4, p. 309, pl. 25, figs. 8, 26; E. B. BRANSON, 1938, idem, vol. 13, no. 3, p. 182; ——, et al., 1938, idem, vol. 13, no. 4, pp. 132, 146, pl. 33, fig. 15; pl. 34, fig. 37; KNECHTEL & HASS, 1938, Jour. Paleontology, vol. 12, p. 519; COOPER, 1939, idem, vol. 13, pp. 400, 420, pl. 39, figs. 11, 12; HASS, 1943, idem, vol. 17, p. 308; E. B. BRANSON & MEHL, and E. R. BRANSON, in E. B. BRANSON, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 221, pl. 32, figs. 51, 52; pl. 39, fig. 37; YOUNGQUIST & PATTERSON, 1949, Jour. Paleontology, vol. 23, p. 64, pl. 17, figs. 4, 5, 9, 13; THOMAS, 1949, Geol. Soc. America Bull., vol. 60, p. 411.

Polgnathus inornata (sic.) THOMAS, 1949, Geol. Soc. America Bull., vol. 60, p. 436, pl. 3, fig. 36.

Blade short relative to length of platform, thin, composed of about four or five denticles. Margins of platform deflected orad, "subparallel to about the posterior third of platform, thence converging to a sharp posterior end which is continued beyond the plate proper by the combined carina and keel." (E. R. Branson, 1934, p. 309). Outer margin of platform higher than inner.

In oral outline at least, the specimen shown by figure 11 seems similar to one described from the Prospect Hill sandstone (Youngquist and Patterson, 1949, pl. 17, fig. 9), and to the cotypes. As has been pointed out in the literature, this species is closely related to *P. lobata* of the Chouteau. The distinction is said to be that at maturity the latter bears a "postero-lateral lobe on the outer flange of the plate (pl. 34, fig. 45)" (Branson and Mehl, 1938, in Branson). The Wassonville specimen has a nearly smooth aboral surface, with only a slight keel on the platform and a small escutcheon. No trace of a postero-lateral lobe on the outer flange of the platform is apparent in oral or aboral view. Presumably this specimen belongs in *P. inornata*. In oral view, *P. lobata* of Thomas (1949, p. 3, fig. 11, not described) from the English River sandstone is similar to the representatives of *P. inornata* from the Prospect Hill and Wassonville. Clearly *P. lobata* and *P. inornata* are closely related. Figures 17 and 18 show a specimen with one margin of the plate only slightly higher than the other. Although fractured distally, the short blade of this species can be inferred in lateral view from figure 18.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also reported from the English River and Prospect Hill sandstones of the same State; Bushberg, Hannibal and Chouteau strata in Missouri; a "Bushberg-Hannibal horizon" in Oklahoma; and a thin shale (Kinderhook) at the base of the Lodgepole limestone, Little Rocky Mountains, Montana.

Figured specimens.—State Univ. of Iowa 4194 (fig. 11), 4195 (figs. 17, 18).

POLYGNATHUS SAGITTARIA
Youngquist & Patterson
Plate 111, figures 7–9

Polygnathus sagittaria YOUNGQUIST & PATTERSON, 1949, Jour. Paleontology, vol. 23, p. 66, pl. 15, figs. 9, 10; pl. 16, fig. 13.

? *Polygnathus symmetrica* COOPER [not E. R. Branson], 1939, Jour. Paleontology, vol. 13, p. 404, pl. 41, figs. 50, 51.

Figured specimen low, elongate in lateral profile, only moderately arched. Blade strongly keeled, composed of about eight subequal denticles which are laterally compressed and confluent essentially to their apices. In oral view, platform convex on inner margin, except for anteriormost portion; outer margin convex in anterior half; slightly concave in oral view along posterior half. Carina prominent, moderately nodose, grades smoothly into blade. Platform is strongly keeled aborally (fig. 8), and bears moderately large subcircular escutcheon. Oral surface of platform bears numerous moderate sized rugae oriented essentially normal to long axis of specimen. Margins of platform deflected orad at angle of about 45° from horizontal.

This species is particularly characterized by its low, elongate profile in lateral view, and the even-sized denticles in the relatively low and strongly keeled blade. In oral and aboral views, at least, the form described as *P. symmetrica* n. sp. in 1939, appears to be similar. The name applied in 1939 seems to have been preoccupied by *P. symmetrica* E. R. Branson, 1934.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also known from the

Prospect Hill sandstone of the same State, and possibly occurs in a "Bushberg-Hannibal horizon" in Oklahoma.

Figured specimen.—State Univ. Iowa 4196.

POLYGNATHUS aff. SYMMETRICA
E. R. Branson
Plate 111, figure 6

Loss of blade from this specimen precludes specific identification, but it closely resembles several forms from Kinderhook strata. In many details it suggests *P. symmetrica* E. R. Branson from the Hannibal of Missouri, but the slightly sinuous carina presumably differentiates it from that species. Other similar forms include *P. lanceolata* of Branson and Mehl (Branson et al., 1938, pl. 34, fig. 42) from the Chouteau of Missouri, and *P. flabellum* of Cooper (1939, pl. 39, figs. 13, 14) from Kinderhook strata in Oklahoma.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimen.—State Univ. Iowa 4197.

PRIONIODUS BARBATUS
Branson & Mehl
Plate 111, figure 10

Prioniodus barbatus BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, p. 288, pl. 23, figs. 19, 20; BRANSON, 1938, idem, vol. 13, no. 3, p. 181; —— & MEHL, in Branson, 1938, idem, vol. 13, no. 4, p. 144, pl. 33, fig. 38; pl. 38, figs. 28, 32; COOPER, 1939, Jour. Paleontology, vol. 13, pp. 405, 420, pl. 46, figs. 17, 18; BRANSON & MEHL in Branson, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 221, pl. 32, fig. 38; pl. 39, figs. 28, 32; THOMAS, 1949, Geol. Soc. America Bull., vol. 60, p. 411, pl. 4, fig. 26.

Bar much compressed laterally; denticles sheathed by bar material for most of their length. Erupted denticles generally in alternating series with elongate germ denticles. Cusp wide, rounded on inner, flattened on outer side, straight particularly along anterior margin in lateral view. Anticusp projects directly abroad without being offset from cusp. Posterior oral margin of anticusp flared laterally along inner side, smooth on outer margin.

This specimen resembles forms illustrated from the Chouteau and English River and from Bushberg-Hannibal strata in Oklahoma somewhat more closely than the cotypes from the Bushberg of Missouri. Particularly in one cotype (fig. 19) the denticles tend to encroach in an orad direction on the posterior side of the cusp whereas in other specimens the cusp is more definitely delimited from the denticles. Also, the outer side of the cusp tends to be more nearly flat in the Wassonville specimen than in the cotype. Presumably these differences have been interpreted as varietal rather than specific, and we are so regarding them.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also reported from the English River and Prospect Hill sandstones of the same State; Bushberg and Chouteau strata in Missouri; and a "Bushberg-Hannibal horizon" in Oklahoma.

Figured specimen.—State Univ. Iowa 4198.

SIPHONODELLA DUPLICATA
(Branson & Mehl)
Plate 111, figure 21

Siphonognathus dupiicata E. B. BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, pp. 295, 296, 297, pl. 4, figs. 16, 17; E. R. BRANSON, 1934 [1933], idem, vol. 8, no. 4, p. 315, pl. 25, figs. 1, 13–16; E. B. BRANSON, et al., 1938, idem, vol. 13, no. 4, pp. 131, 133, 136, 148, pl. 33, fig. 17; pl. 34, figs. 34, 35; KNECHTEL & HASS, 1938, Jour. Paleontology, vol. 12, p. 519; HASS, 1943, idem, vol. 17, p. 308; E. B. BRANSON & E. R. Branson in E. B. Branson, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 222, pl. 32, fig. 17; pl. 39, figs. 34, 35.

Polygnathus plana HUDDLE, 1934, Bull. Am. Paleontology, vol. 21, no. 72, pp. 17, 103–104, pl. 8, figs. 39–43.

Siphonognathus quadruplicata [part] COOPER, 1939, Jour. Paleontology, vol. 13, pp. 409–420, pl. 41, figs. 44, 45.

Siphonodella duplicata E. B. BRANSON & MEHL in Shimer and Shrock, 1944, Index fossils of North America, p. 245; YOUNGQUIST & PATTERSON, 1949, Jour. Paleontology, vol. 23, pp. 69, 71, pl. 16, figs. 7–10; THOMAS, 1949, Geol. Soc. America Bull., vol. 60, pp. 409, 410, 412, 414, pl. 3, figs. 8, 9.

Representatives of *Siphonodella* are conspicuous in the Wassonville conodont assemblage. Most of them are fragmentary (usually the blade is broken away) but a single well preserved individual typically illustrates *S. duplicata*.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also known from the English River and Prospect Hill sandstones of the same State. It has been recorded from Bushberg, Hannibal and Chouteau beds of Missouri; a "Bushberg-Hannibal horizon" and the Welden in Oklahoma, a thin shale (Kinderhook) at the base of the Lodgepole limestone, Little Rocky Mountains, Montana; and the basal Rockford of Indiana.

Figured specimen.—State Univ. Iowa 4199.

SIPHONODELLA QUADRUPLICATA
(Branson & Mehl)
Plate 111, figures 22–25

Siphonognathus quadruplicata E. B. BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, pp. 295–296, 297, pl. 24, figs. 18, 21; E. R. BRANSON, 1934 [1933], idem, vol. 8, no. 4, p. 315; E. B. BRANSON, 1938, idem, vol. 13, no. 3, p. 182; ——, et al., 1938, idem, vol. 13, no. 4, p. 131, pl. 33, figs. 57, 58; KNECHTEL & HASS, 1938, Jour. Paleontology, vol. 12, p. 519; [part] COOPER, 1939, idem, vol. 13, pp. 409, 420, [not pl. 41, figs. 44, 45]; HASS, 1943, idem, vol. 17, p. 308; E. B. BRANSON & MEHL in E. B. Branson, 1944, Missouri Univ. Studies vol. 19, no. 3, p. 222, pl. 32, figs. 57, 58.

Polygnathus newalbanyensis [part] HUDDLE, 1934, Bull. Am. Paleontology, vol. 21, no. 72, pp. 17, 101, pl. 8, figs. 27, 28?, not 26.

Siphonognathus newalbanyensis [part] COOPER, 1939, Jour. Paleontology, vol. 13, pp. 409, 420, pl. 41, figs. 21, 22.

Siphonodella quadruplicata E. B. BRANSON & MEHL in Shimer and Shrock, 1944, Index fossils of North America, p. 245, pl. 94, figs. 44, 45; YOUNGQUIST & PATTERSON, 1949, Jour. Paleontology, vol. 23, pp. 70, 71, pl. 16, fig. 11; THOMAS, 1949, Geol. Soc. America Bull., vol. 60, pp. 409, 410, 412, 414, pl. 3, figs. 2, 3, 6.

Representatives of this species are not uncommon in the Wassonville and show "considerable variation of size, shape, and ornamentation" as do those discussed by Thomas (1949, p. 409) from the English River and Prospect Hill strata. They all, however, have two ridges on the lateral zone of the anterior end of the platform on at least the outer side of the carina, and frequently on both sides. Our largest specimen is illustrated to show the smooth aboral surface, slight keel and nearly complete lack of a distinct escutcheon.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Also known from the English River and Prospect Hill sandstones of the same State; from Bushberg and Hannibal beds in Missouri; the upper New Albany shale of Indiana; the upper Sunbury shale of Ohio; a "Bushberg-Hannibal horizon" in Oklahoma; and a thin shale (Kinderhook) at the base of the Lodgepole limestone, Little Rocky Mountains, Montana.

Figured specimens.—State Univ. Iowa 4200 (fig. 22), 4201 (figs. 23–25).

SOLENODELLA TENERA (E. R. Branson)?
Plate 111, figure 3

? *Solenognathus tenera* E. R. BRANSON, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, pp. 332–333, pl. 27, fig. 8; E. B. BRANSON, and E. B. BRANSON & MEHL, respectively in Branson et al., 1938, idem, vol. 13, no. 4, pp. 132, 140, pl. 34, fig. 14; —— & ——, in E. B. Branson, 1944, idem, vol. 19, no. 3, p. 222, pl. 39, fig. 14.

? *Solenodella tenera* THOMAS, 1949, Geol. Soc. America Bull., vol. 60, p. 412, pl. 3, figs. 18, 20.

Specimen relatively thin and blade-like, essentially smooth on inner (unfigured) side except for a small anterior-posterior ridge just orad of keel. Outer side of blade differentiated into denticles fused essentially to their apices. Denticles larger, more numerous anterior than posterior to cusp. Cusp relatively small. Escutcheon conspicuous, in shape of broad isosceles triangle with longer side along inner margin of specimen, and obtuse apex just beneath cusp on outer side.

The figured specimen appears to resemble the particular individual referred to *S. tenera* by Branson and Mehl from the Chouteau. Superficially the anterior end of our specimen seems to differ from the Chouteau form, but this is because its two anterior denticles have been broken away. The holotype seems to differ slightly from our form

and the Chouteau specimen in the larger number of denticles composing the blade, the greater height of the blade, and the more prominent cusp. These differences do not seem to have been regarded as significant.

Occurrence.—Wassonville dolomite, Washington County, Iowa. Similar forms are known also from the English River and Prospect Hill sandstones of the same State, and from Hannibal and Chouteau strata in Missouri.

Figured specimen.—State Univ. Iowa 4202.

SPATHOGNATHODUS MACER
(Branson & Mehl)
Plate 111, figures 1, 2

Spathodus macer BRANSON & MEHL, 1934 [1933], Missouri Univ. Studies, vol. 8, no. 4, p. 276, pl. 22, fig. 19; BRANSON, 1938, idem, vol. 13, no. 3, p. 182.
Spathognathodus macer BRANSON, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 221.

Blade thin, slightly bowed and arched, low posteriorly and high anteriorly. Denticles numerous, usually about 25. Largest denticles anterior. Escutcheon shallow.

Our two specimens might be regarded as a new species, but we are reluctant to name them. They appear to be somewhat different in general form, but we cannot adequately delimit them from *S. macer* Branson & Mehl. Numerous Lower Mississippian species of *Spathognathodus* have already been described and they seem to have been interpreted so broadly as to leave little room for additional species. The Wassonville specimens seem to us to be most similar to *S. macer*, but they also resemble such other Kinderhook conodonts as the paratype of *S. elongatus* from the Chouteau (Branson and Mehl, 1938, pl. 35, fig. 9) and *S. strigosus* (Thomas, 1949, pl. 4, fig. 15) from the Prospect Hill sandstone.

Occurrence.—Wassonville dolomite, Washington County, Iowa.

Figured specimens.—State Univ. Iowa 4203 (fig. 1), 4204 (fig. 2).

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EXPLANATION OF PLATE 111

All specimens are from the lower portion of the Wassonville dolomite in the south bluff of English River, Washington County, Iowa. All ×40.

FIGS. *1, 2*—*Spathognathodus macer* (Branson & Mehl). Outer lateral views of two specimens. (p. 791)

3—*Solenodella tenera* (E. R. Branson)? Outer lateral view of a nearly complete individual. (p. 790)

4, 5—*Polygnathus communis* Branson & Mehl. Blade incomplete distally. See also figs. *19, 20*. (p. 787)

6—*Polygnathus* aff. *symmetrica* E. R. Branson. (p. 789)

7–9—*Polygnathus sagittaria* Youngquist & Patterson. Outer lateral, aboral, and oral views of a well preserved specimen. (p. 788)

10—*Prioniodus barbatus* Branson & Mehl. Outer lateral view of an incomplete specimen. (p. 789)

11—*Polygnathus inornata* E. R. Branson. See also figs. *17, 18*. (p. 787)

12, 13—*Hibbardella* sp. Inner and outer views of two specimens. (p. 786)

14—*Hindeodella* sp. A fragmentary individual in outer lateral view. (p. 787)

15—*Hindeodella* aff. *echinata* E. R. Branson. (p. 786)

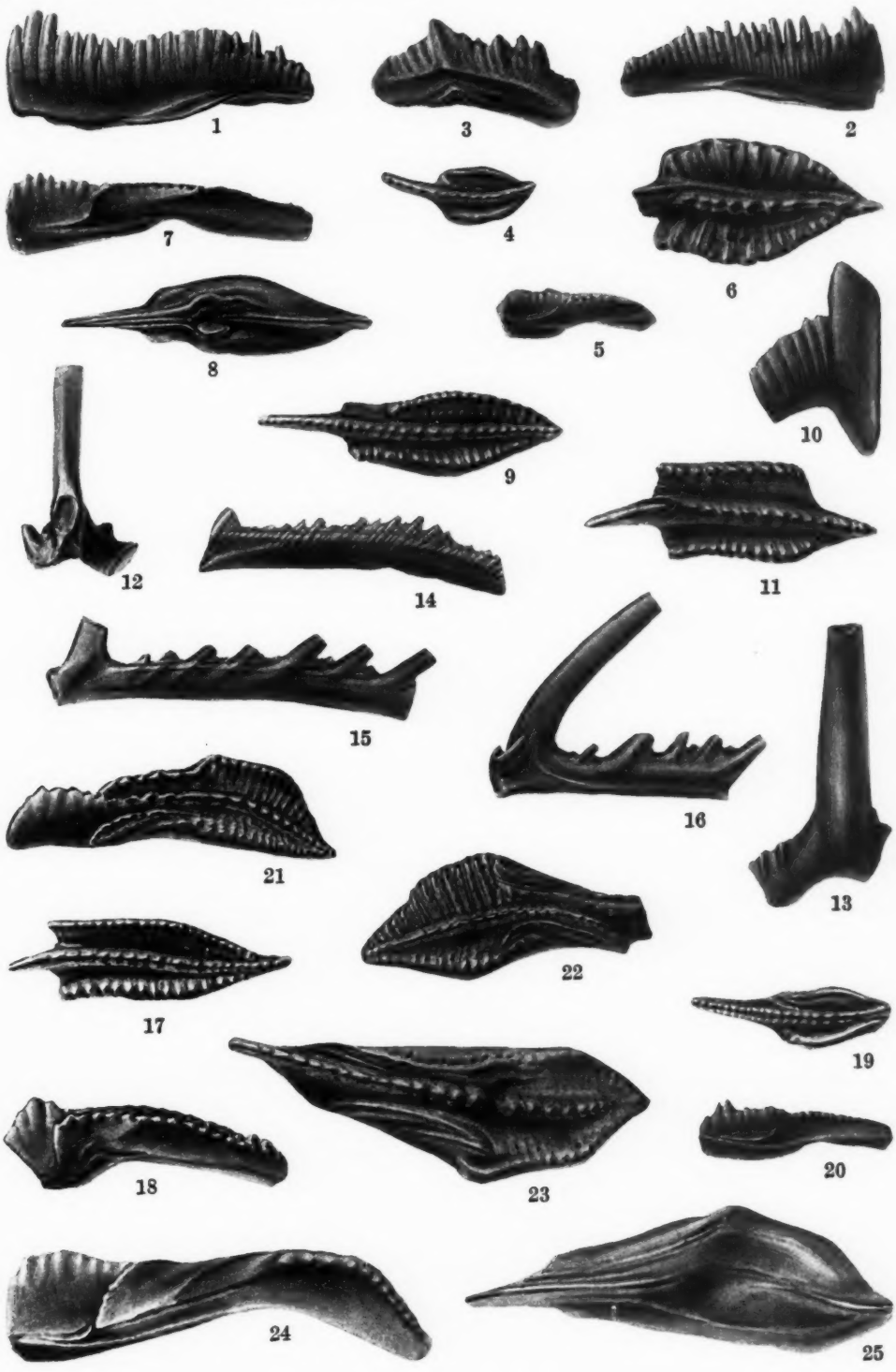
16—*Ligonodina* sp. Inner lateral view. (p. 787)

17, 18—*Polygnathus inornata* E. R. Branson. See also fig. *11*. (p. 787)

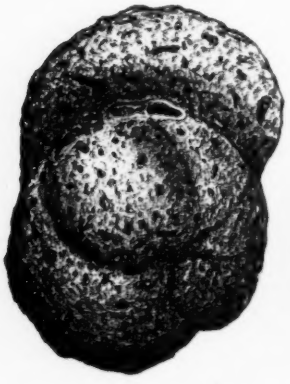
19, 20—*Polygnathus communis* Branson & Mehl. See also figs. *4, 5*. (p. 787)

21—*Siphonodella duplicata* (Branson & Mehl). Inner oblique view of a complete specimen. (p. 789)

22–25—*Siphonodella quadruplicata* (Branson & Mehl). Two specimens. Figures *23–25* are the same individual. (p. 790)



Youngquist and Downs, Lower Mississippian conodonts



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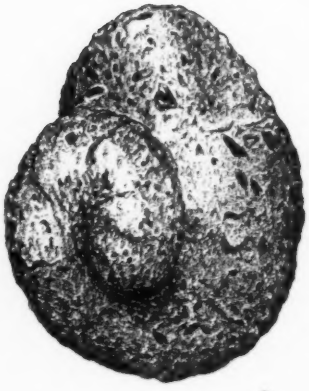

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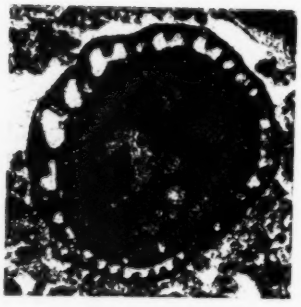

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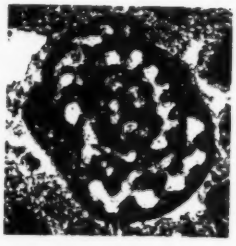

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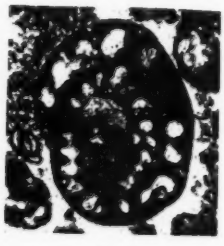

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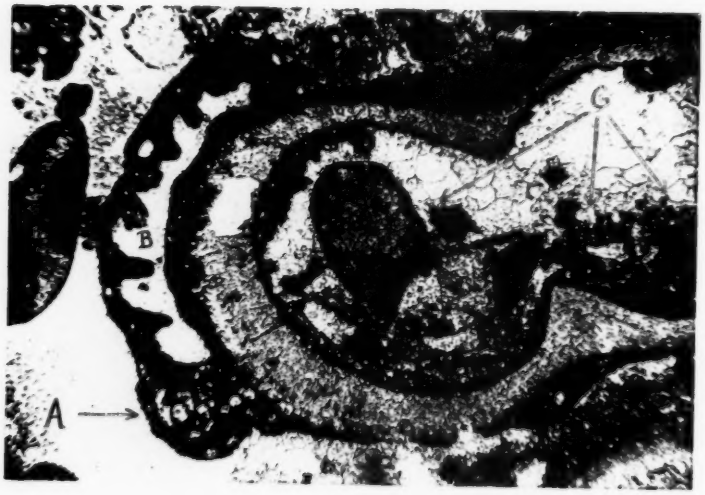

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Weynschenk, Foraminifera

JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, PP. 793–795, PL. 112, 3 TEXT FIGS., NOVEMBER 1951

TWO NEW FORAMINIFERA FROM THE DOGGER AND UPPER TRIASSIC OF THE SONNWEND MOUNTAINS OF TYROL

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ABSTRACT—*Labyrinthina mirabilis*, n. gen., n. sp., is described from the Upper Triassic of western Austria and a Jurassic variety of the modern species *Recurvoides trochamminiforme* Höglund is recorded from the same region. The ecology of these Foraminifera is considered.

INTRODUCTION

THIS paper is a continuation of a former study (Weynschenk, 1950). The Dogger (Middle Jurassic) specimens were obtained from the "Hornsteinbreccia" limestones by crushing, sieving and washing a sample prepared at the Geological Survey of Holland. The Upper Triassic specimens were studied by thin sections of reef limestone, The author is indebted to the Managing Director of the Geological Survey and to Dr. J. H. van Voorthuysen of Haarlem for the opportunity of making this study. Dr. J. Hofker kindly lent for comparison Recent specimens of *Recurvoides trochamminiforme* collected by the Danish Ingolf Arctic Expedition of 1895–96. The specimens described here have been deposited in the collection of the Department of Geology and Paleontology, University of Innsbruck, Austria.

SYSTEMATIC DESCRIPTIONS

Family LITUOLIDAE

Genus LABYRINTHINA Weynschenk, n. gen.

LABYRINTHINA MIRABILIS Weynschenk, n. sp.

Plate 112, figures 4–9; text-figures 1, 2

Test free or attached, oldest chambers irregularly planospiral in one and one-half to two and one-half whorls, later becoming uncoiled (figs. 8A, 9). A globular proloculus (fig. 4P) is followed by a few narrow chambers which widen, become labyrinthic, may be encrusting (figs. 8B, 5), or free and uniserial. The adult chambers may be very large

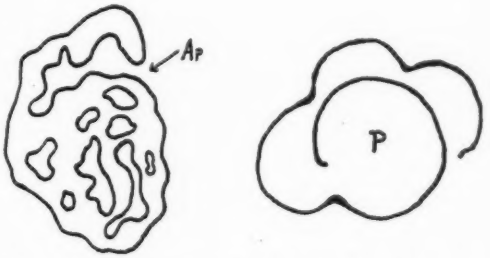

FIG. *1* (left)—Section of *Labyrinthina mirabilis* showing aperture (Ap) at base of last chamber, ×62 5

FIG. *2* (right)—Enlargement of the proloculus and embryonic chambers (P) of *Labyrinthina mirabilis* from specimen shown in plate, figure 4, ×360.

(figs. 8B, 9). Shell surface smooth, arenaceous; wall thick, consisting of very fine calcareous grains and much cement. Aperture at base of final chamber in planospiral speci-

EXPLANATION OF PLATE 112

FIGS. *1–3*—*Recurvoides* cf. *trochamminiforme* Höglund. From the Jurassic of Austria, apertural and side views, ×120. (p. 794)

FIGS. *4–9*—*Labyrinthina mirabilis* Weynschenck, n. gen., n. sp. From the Upper Triassic of Austria. *4*, Section showing globular proloculus, ×47, see text-figure *2*. *5*, Section through specimen encrusting a detrital fragment, ×27. *6*, Transverse section showing irregular labyrinthic chambers, ×26. *7*, Transverse section with oldest chambers not shown because of the shifted axis, ×26. *8*, Section showing: *A*, irregular spiral of oldest chambers; *B*, later uncoiled encrusting chambers; and *G*, detrital sedimentary fragments (redeposit) in cavity indicating very shallow water conditions; ×25. *9*, Section through free uncoiled part of specimen in which last chambers become very broad, ×25. (p. 793)

mens (text-fig. 1, Ap), in uncoiled forms probably terminal in last chamber.

Proloculus 0.052 mm. in diameter. Text-figure 2 shows the arrangement of the embryonic chambers. This diagram is enlarged from plate figure 4P. Dimensions of the specimens illustrated on plate are as follows: figure 6, greatest and smallest diameters, 0.99 mm. and 0.78 mm.; figure 7, 0.96 mm. and 0.70 mm.; figure 8, length, 2.21 mm.; and figure 9, length, 1.04 mm.

All of the specimens were obtained from

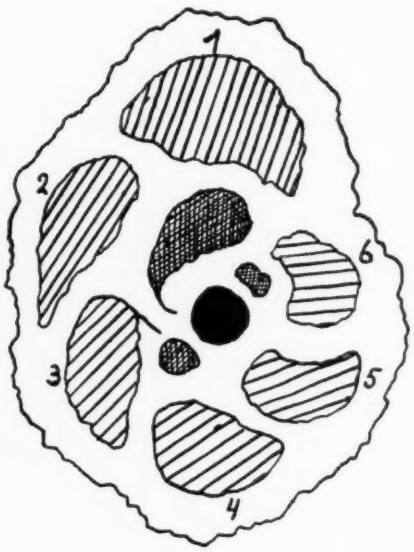

FIG. 3—Section through specimen of *Recurvoides* cf. *trochamminiformе* showing, by direction of ruled lines, shifting of the axis of coiling during growth of last whorl; ×150.

allothegenic Upper Triassic reef limestone in sample 107 from Spieljoch in the Sonnwend Mountains (see Spengler's geological map, 1935).

Associated organisms include *Pseudocyclammina lituus* Yabe & Hanzawa (Weynschenk, 1950, p. 7, pl. 3, fig. 26) which is very abundant, Miliolidae, Textulariidae, Gastropoda and algae. Also a single vertical section of a member of the Verneuilinidae was observed. A specimen of this type has not been reported before from the Upper Triassic.

Labyrinthina mirabilis lived at a depth of only a few meters in oxygen-rich, warm, tropical water. The reef limestone consists of very fine-grained matrix enclosing many detrital fragments. Cavities seem to have been filled with coarse clastic material indicating very shallow water (Sander, 1936; Weynschenk, 1949, pl. 6, fig. 9, pl. 14, figs. 23, 24). No dolomite or glauconite was noted.

Genus RECURVOIDES Earland, 1934
RECURVOIDES cf. TROCHAMMINIFORME Höglund

Plate 112, figures 1–3; text-figure 3

Recurvoides trochamminiformе HÖGLUND, 1947, Zool. Bidrag. Uppsala, Bd. 26, p. 149, pl. 11, figs. 7, 8, pl. 30, fig. 23, text-fig. 120.

Test free, chambers coiled in a twisting spiral of two or three whorls, last volution generally with six chambers. Spiral axis shifting regularly during growth in such a way that the earliest chambers are completely hidden, only those of the last whorl and one or two at the end of the previous volution are visible. During one volution the axis shifted through 60° as shown by the ruling in text-figure 3. Periphery slightly lobulate, wall arenaceous, consisting of dark grains in a calcareous cement, brown colored, thick. Aperture a little above base of apertural face, an oblong slit with lips like those of modern specimens. Specimens vary from 0.39 mm. to 0.53 mm. in diameter and from 0.19 mm. to 0.37 mm. in thickness. The wall is 22μ to 26μ thick. The proloculus is about 0.015 mm. in diameter. This is considerably smaller than the 0.025 mm. of modern specimens from the Skagerak and elsewhere (Höglund, 1947, p. 150). Aside from this difference, the Dogger and modern forms are very similar. Modern specimens generally have a more lobulate periphery but some cannot be distinguished, as not only the shape but also the color and structure of the test are identical. Jurassic specimens are known only in the northwestern part of the Dalfazer Joch from a small outcrop of the "Hornsteinbreccia" on the west side of the road from Klobenjoch to Streichkopf (see Spengler's geological map, 1935). They are of middle to upper Dogger age.

Associated fossils include corals, Miliolidae, Peneroplidae, Lituolidae and Ventrolaminidae (Weynschenk, 1950, pp. 26–28). These suggest a temperature of 20°C. or

more rather than the 6° or 7° of Gullmarfjord where modern specimens have been collected.

Other ecological conditions seem to have been much the same. The faunal assemblage and lithology indicate water not more than 10 meters deep and the "Hornsteinbreccia" is believed to have accumulated at a depth of less than 50 meters (Weynschenk, 1949, p. 29). Specimens now living in Gullmarfjord occur at a depth of 15 meters or less.

TABLE 1—COMPARISON OF JURASSIC AND RECENT FORMS OF *Recurvoides trochamminforme*

	Number of studied individuals	Test diameter (mm.)	Test thickness (mm.)	Test sculpture	Wall thickness	Proloculus diameter	Depth temperature
Dogger Sonnwend Mountains	14	0.39–0.53	0.19–0.37	slightly lobulated	22μ–26μ	±15μ	shallow warm
Recent Ingolf Arctic Exp.	20	0.20–0.58	0.20–0.39	very lobulated	20μ–26μ	±25μ	deep cold
Recent Skagerak Höglund	—	0.11–0.35	0.07–0.24	very lobulated	4μ–8μ	±25μ	shallow to deep cold

The bottom of the Dogger sea in the Dalfazer Joch consisted of limestone fragments mostly up to 5 cm. in diameter and grains of detrital dolomite 2 mm. to 3 mm. in diameter embedded in lime mud (Weynschenk, 1949, figs. 2–4). Silicification of the sediment seems to have begun during the early stages of its consolidation (Weynschenk, 1949, chap. 2) and indicates the presence of dissolved silica in fairly clear tropical water. The bottom of the Gullmarfjord consists of much gravel mixed with very fine mud containing considerable organic material.

The Dogger forms are very similar to modern specimens and these Foraminifera, in spite of their complexity, evidently were very stable for a long period of time.

Haplophragmium turbinatum Brady (1873–1876, pl. 35, fig. 9), referred to *Trochammina* by Cushman (1948, pl. 5, fig. 2), is a closely related species.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, PP. 796–807, PLS. 114, 115, 1 TEXT FIG., NOVEMBER 1951

OSTRACODA FROM THE UPPER JURASSIC REDWATER SHALE MEMBER OF THE SUNDANCE FORMATION AT THE TYPE LOCALITY IN SOUTH DAKOTA[1]

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ABSTRACT—Nine species of Ostracoda, all of them apparently marine, are described from the Redwater shale member of the Sundance formation, Upper Jurassic (Oxfordian), at its type locality, Butte County, South Dakota. The following genera are represented in the collection: *Paraparchites?* Ulrich & Bassler, *Eridoconcha* Ulrich & Bassler, *Apatocythere?* Triebel, *Progonocythere* Sylvester-Bradley, *Monoceratina* Roth, *Leptocythere* Sars, *Cytheridea?* Bosquet and *Cytherura?* Sars.

INTRODUCTION

THE present paper is the first of a series devoted to the description of marine Jurassic Ostracoda from the western interior United States.

All the microfossil samples were collected by R. W. Imlay and A. R. Loeblich, Jr., and the ostracodes described here were sorted by Dr. Loeblich. Loeblich and Tappan (1950) have described 56 species of Foraminifera from the type locality of the Redwater shale member of the Sundance formation, in the first of a series of their studies on North American Jurassic Foraminifera.

The following quotation from Loeblich and Tappan (1950, p. 40) gives location and stratigraphic information about the type Redwater:

> Type section of the Redwater shale member of the Sundance formation, one-half mile north of Redwater Creek opposite the mouth of Crow Creek, about 7 miles northwest of Spearfish, in the S. ½, sec. 2, T. 7 N., R. 1 E., Butte County, S. Dak. Measured by R. W. Imlay and William Saalfrank in June 1945. Microfossil samples collected September 21, 1948, by R. W. Imlay and A. R. Loeblich, Jr.
>
> | | Feet |
> |---|---|
> | Morrison formation, basal part | |
> | 5 to 10 feet of soft yellow sandstone, overlain by dark gray shale containing small calcareous pellets. | |
> | Sundance formation | |
> | Redwater shale member: | |
> | Shale, in part silty near base, soft, dark gray; contains many pieces of selenite and abundant belemnites; lenses of sandy limestone present at several levels, many fossiliferous limestone concretions in upper half. U. S. G. S. Mesozoic collection 19570, made 55 feet above the base in lens of sandy limestone, contains *Cardioceras* (*Scarburgiceras*) *cordiforme* (Meek and Hayden), *C.* (*S.*) *wyomingense* Reeside, *Grossouvria* (*Poculisphinctes*) cf. *G. trinys* (Buckman) and other fossils. Twelve microfossil samples were collected from this unit as follows: J-50a, 5 to 15 feet above base of unit; J-50b, 15 to 22 feet; J-50c, 22 to 33 feet; J-50d, 33 to 41 feet; J-50e, 41 to 48 feet; J-50f, 48 to 55 feet; J-50g, 55 to 62 feet; J-50h, 62 to 68 feet; J-50i, 68 to 75 feet; J-50j, 75 to 82 feet; J-50k, 82 to 87 feet; J-50l, 87 to 108 feet above base of unit | 118 |
> | Sandstone, soft, medium yellow, shaly to thick bedded | 6 |
> | Shale and sandy shale, soft, gray. Sample J-49 (barren of Foraminifera) | 10 |
> | Sandstone, soft, yellow | 1 |
> | Shale, soft, gray. Sample J-48 (barren of Foraminifera) | 1 |
> | | 136 |
> | Lak member: | |
> | Shale, light red, weathers pinkish; contains 2 feet of soft white sandstone about 24 feet above base | 50 |

The Redwater shale member includes in its lower portion the *Cardioceras cordiforme* zone, stratigraphically the highest ammonite zone recognized in the Western Interior Jurassic. Imlay (1947, p. 261) has indicated that the zone represents most of the *mariae* zone of northwest Europe. On the basis of the widespread occurrence of *Cardioceras* and associated mollusks, Imlay has correlated the Redwater with the Stump sandstone of eastern Idaho and western Wyoming, the Curtis formation of Utah, the Swift formation of Montana, and the "Upper Sundance" of central Wyoming.

[1] Published by permission of the Director, U. S. Geological Survey.

Marine Jurassic Ostracoda have not been described previously from the western interior United States. Morey (1931) reported in abstract the occurrence of *Cythere* O. F. Müller and *Cytherella* Bosquet from the Sundance formation of Wyoming, and according to E. B. Branson (personal communication, 1945), a graduate student at the University of Missouri several years ago prepared a thesis on some Sundance ostracodes.

Very little work has been done on the marine Jurassic ostracodes of the United States. Swain (1946) and Swartz and Swain (1946) have described species from the Schuler formation, Upper Jurassic of the Gulf region. Calahan (1939) and Swain (1949) illustrated, but did not formally describe, some additional ostracodes from the Schuler formation.

European literature contains relatively few articles on marine Jurassic ostracodes. Among the more important are those by Terquem (1885, 1886), Issler (1908), Jones and Sherborn (1888), Waagen (1866), Gümbel (1871), Schick (1903), Chapman (1900), Jones (1884), Triebel and Bartenstein (1938), Sylvester-Bradley (1948) and Brand (1949).

Most of the above European publications deal with Middle Jurassic ostracodes, so perhaps it is not surprising that the present small fauna exhibits a somewhat closer relationship to the Middle Jurassic than to the Upper Jurassic. It is important to notice, however, that none of the diagnostic Upper Jurassic ostracodes of the Gulf region, even at the generic level, occur in the type Redwater. This evidence is in support of Imlay's conclusion (1950, p. 73) that there was never a direct connection between the Upper Jurassic seas of the western interior United States and those of the Gulf region. The correlation of the Redwater shale with the Oxfordian stage, middle Upper Jurassic of Europe, is based upon the occurrence of the characteristic Oxfordian ammonite *Cardioceras* Neumayr & Uhlig in the lower part of the Redwater (Imlay, 1947, p. 261).

The writers extend their thanks to A. R. Loeblich, Jr. of the U. S. National Museum, and to R. W. Imlay, J. B. Reeside, Jr. and W. D. Quinlivan of the Geological Survey for their contributions to this study.

In the following descriptions, under "Occurrence" the numbers refer to horizons indicated in the foregoing measured section. The type specimens are deposited in the U. S. National Museum.

DESCRIPTION OF SPECIES

Family LEPERDITELLIDAE Ulrich & Bassler, 1906

Genus PARAPARCHITES Ulrich & Bassler, 1906

Shell small, leperditoid, subrhomboidal or subovate; greatest height about median; greatest thickness near middle or anterior part of shell; dorsal margin moderately convex; ventral margin gently convex; anterior margin slightly more broadly rounded than posterior. Right valve larger than left and overlapping it along free margins; hinge margin of left valve straight, commonly overlapping the right or receiving its edge in a shallow groove. Surface moderately convex, smooth or ornamented. Many species have a smooth spine or horn-like protuberance near the anterodorsal angle. Hinge line straight or very slightly curved, simple.

Type species.—Paraparchites humerosus Ulrich & Bassler.

Discussion.—Paraparchites differs from *Aparchites* Jones only in that the latter shows neither the ventral and dorsal overlap nor the anterodorsal spine of the former. It is likewise similar to *Leperditella* Ulrich except for the presence of a broad dorsomedian depression on the valve surface and the larger left valve characteristic of the latter. According to I. G. Sohn (personal communication), Marliére (1948) described a questionable *Paraparchites* species from post-Paleozoic portion of the Karoo system in Africa. Aside from this, it has previously been reported only from rocks of Paleozoic age.

PARAPARCHITES? sp.

Plate 113, figures 1, 2

Left valve subovate in lateral view; dorsal

margin moderately convex, with greatest height slightly anteromedian; ventral margin slightly convex, straightened medially; anterior margin broadly and nearly uniformly rounded; posterior margin more narrowly rounded, extended slightly ventrad of midheight, subtruncate above. Valve moderately convex; greatest thickness slightly posterior and dorsad of middle. Shell wall thick. Surface of valve recrystallized but apparently smooth.

Hinge margin of left valve straight, about half of shell length; dorsad of hinge, surface of valve projects as a broad low umbo. Hinge surface bears an anterior elongate shallow socket, an interterminal weak narrow groove, and a posterior obscure socket. Inner lamellae lacking. Muscle scar not observed.

Length, 0.96 mm., height, 0.67 mm.

Relationships.—In general shape, smooth surface, straight hinge and lack of calcified inner lamellae this form is related to the family Leperditellidae Ulrich & Bassler (1906), and perhaps represents an example of *Paraparchites* Ulrich & Bassler. As here oriented the more broadly rounded end is considered to be the anterior. Some other authors, for example Kellett (1933, pp. 64–67), have considered the more narrowly rounded end to be anterior. The hinge of the present form suggests an advancement beyond the simple leperditellid hinge structure, but the lack of an inner lamella and of ventral median incurvature of the valve margin prevent assignment to the Cypridae or the Cytheridae.

Occurrence.—Sample J-50b, 33 to 50 feet above base of Redwater shale: USNM 106635.

Genus ERIDOCONCHA
Ulrich & Bassler, 1923

Original description.—Small, apparently unequivalved carapaces with concentric, simple or rugose bands or rows of punctae, resembling an equilateral pelecypod or a brachiopod in shape and markings.

Type species.—*Eridoconcha rugosa* Ulrich & Bassler.

Levinson (1950) investigated the hingement of *Eridoconcha rugosa* and noted on one of the valves the presence of a ridge, with a prominent dorsojacent and a fine ventrojacent groove, running the length of the dorsal margin. He found no hinge features on the opposite valve. Regarding orientation, he stated:

> There are neither spines, "brood pouches," thinning of the shell wall, differences in thickness, nor dentition to aid in the determination of orientation; there is only a tendency for one end of the valve to be a little more pointed. The pointed end is referred to as the antiplenate and until additional criteria are put forth the valves are regarded as right- and left-plenate.

Ulrich and Bassler (1923) place *Eridoconcha* in the family Aparchitidae, and Bassler and Kellett (1934) place it in the Leperditellidae. Levinson (1950) suggested that it be placed in the Primitiidae on the basis of similarity in hingement and the presence of sulcation. The writers are inclined to agree that *Eridoconcha* probably should be separated from the Leperditellidae, but are uncertain as to its placement in the Primtiidae. The present examples, at least, are not sulcate and bear no median pit, and are not at all closely related to the primitiids.

ERIDOCONCHA MONOPLEURA
Swain & Peterson, n. sp.
Plate 113, figures 6–9

Shell subovate or subelliptical in lateral view; highest medially; hinge margin slightly convex, truncate medially, about two-thirds of shell length; ventral margin moderately convex; terminal margins broadly and nearly equally rounded, the margin here considered as posterior, extended farther beyond end of hinge than anterior. Left valve larger than right; in interior view, ventral portion of left valve bears a slight groove, just within outer margin, for reception of edge of right. Exterior of right valve moderately convex; that of left valve weakly convex; greatest thickness mid-dorsal. Inner concavity of valves shallow, not equalling convexity of outer surface, particularly in right valve.

Surface bears a broad, low, median concentric ridge extending to each cardinal angle; near its termination ridge gradually narrows and curves sharply to conform with outer margin of valve; at end here considered to be anterior, ridge curves toward dorsum more abruptly than at opposite end, a feature apparent only on close examination in present examples. Surface otherwise unornamented.

Hingement not clearly observed, but apparently is simple and consists in right valve of a weak narrow groove running the length of hinge; in left valve is a corresponding low narrow bar with dorsojacent obscure groove. Inner lamellae lacking. Muscle scar not observed.

Length of right valve cotype, 0.57 mm.; height, 0.40 mm.; thickness, 0.12 mm. Length of left valve cotype, 0.67 mm.; height, 0.45 mm.; thickness, 0.07mm.

Relationships.—The concentric surface ornamentation, straight hinge, lack of inner lamellae, and general shape ally this species with *Eridoconcha* Ulrich & Bassler (1923), a form not previously reported from strata younger than Devonian (Bassler and Kellett, 1934, p. 16). That genus typically has pronounced dorsal umbos that are lacking in the present species.

Recent study of some species of *Eridoconcha* by Levinson (written communication), as well as by Keenan (Levinson, written communication) and by Swain and E. J. Bolin, has shown that the concentric ridges represent the edges or surfaces, as the case may be, of instar valves not shed by the growing *Eridoconcha*. The external convexity greater than is matched by internal concavity results from the piling up of successive molts, frequently with unoccupied space between them.

The present examples may not represent the complete form, but in the three specimens at hand it is possible that each represents two growth stages; that the ventral margin of the median concentric ridge is the margin of the shell of an immature instar that has been retained on the adult shell. The dorsal margin of the concentric ridge may represent the position of the ventral edge of a still younger instar shell that was lost in diagenesis or was actually molted during growth of the intermediate instar. In the writers' collections from the Ordovician Maquoketa shale, the umbonation in examples of *Eridoconcha* depends upon the presence of the third small shell in the middorsal portion of each adult shell.

The unequal external convexity of the two valves in *E. monopleura* cannot be fully evaluated from the three separated valves at hand, but this feature in conjunction with the single concentric ridge seems to provide basis for separation from other described species.

Occurrence.—Sample J-50b, 33 to 50 feet above base of Redwater shale. Cotypes, USNM 106637 and 106638; paratype, USNM 106636.

Family CYTHERIDAE Baird, 1850
Genus APATOCYTHERE Triebel, 1940
APATOCYTHERE? LOEBLICHORUM
Swain & Peterson, n. sp.
Plate 113, figures 3–5

Shell ovoid in lateral view; highest approximately at midlength; dorsal margin strongly convex, sloping somewhat more steeply behind than in front of position of greatest height; ventral margin moderately convex; terminal margins rounded, the anterior narrower and slightly more extended than posterior. Left valve larger than right, extending strongly beyond the other along ventrum, less strongly elsewhere. Valves moderately convex, greatest thickness median to slightly post-median. Surface coarsely but weakly pitted. Shell wall rather thick, with exterior polished in better preserved specimens.

Hinge of right valve about two-thirds of shell length, consisting of a rabbet-groove of which the step portion is about parallel to valve margin, and the riser is bounded by dorsal margin of valve; at either end of groove valve margin slightly elevated to form obscure tooth-like processes. Hinge of left valve consists of terminal obscure socket-like, elongate depressions and an interterminal narrow ridge that forms ventral boundary of a rabbet-groove. Inner lamellae narrow; line of concrescence and inner margin apparently coincide. Radial canals few

and widely spaced. Muscle scar consists of an anteromedian vertical row of four spots and at least one additional anterior spot.

Length of holotype (pl. 113, fig. 3), 0.49 mm.; height, 0.366 mm.; thickness, 0.25 mm.

Relationships.—This species is related to *Apatocythere* Triebel and an undescribed Cretaceous genus. The hinge of *Apatocythere* consists in the right valve of an anterior non-crenulate rounded tooth, an interterminal bar and a posterior smooth, elongate, small tooth; in the left valve there are corresponding terminal smooth sockets, an interterminal groove dorsad of which is a prominent accommodation groove (Triebel, 1940, pl. 9). The muscle scar in that genus consists of a vertical row of four spots and a single, more anterior spot. The inner lamellae are broader and the radial canals more numerous than in the present species. The obscure non-crenulate terminal teeth and sockets of *A.? loeblichorum* are much less clearly differentiated than in typical *Apatocythere*, and probably should be regarded as representing a more primitive stage in the development of the cytherideid hinge. The differences in the interterminal portions of the hinge also make the assignment of this species to *Apatocythere* very questionable.

The ovoid outline, musculature, and narrow inner lamellae of the present species are strongly reminiscent of an undescribed genus from the Lower Cretaceous of North Carolina, but in that genus there are better differentiated and crenulate terminal hinge teeth and sockets.

Well preserved specimens that are generically related to *A? loeblichorum* are represented in the Redwater shale collections from other localities. When this additional material has been completely studied, it seems probable that a new genus will be erected that will include the present species.

Occurrence.—Sample J-50 k, 100 to 105 feet above base of Redwater shale. Holotype, USNM 106639; paratypes, USNM 106640 and 106641.

Genus PROGONOCYTHERE Sylvester-Bradley, 1948

PROGONOCYTHERE HIEROGLYPHICA Swain & Peterson, n. sp.

Plate 113, figures 10–18

Shell elongate-subrhomboidal in lateral view; hinge margin nearly straight, about two-thirds of shell length, cardinal angles broadly obtuse, the posterior better defined; ventral margin nearly straight, subparallel to dorsum; anterior margin broadly rounded, slightly extended below, subtruncate above; posterior margin extended

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EXPLANATION OF PLATE 113

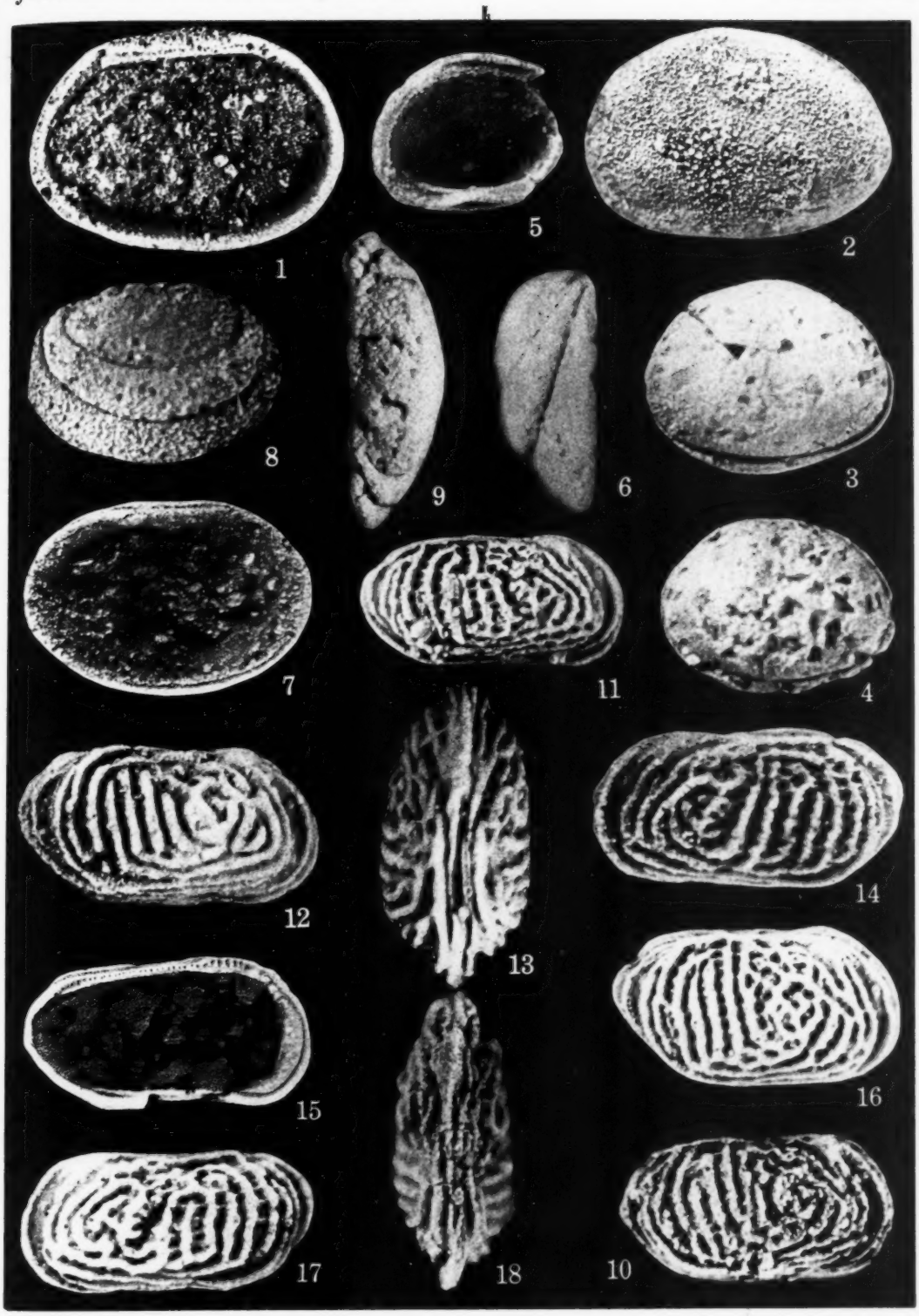
All specimens are from the type locality of the Redwater shale member of the Sundance formation about 7 miles northwest of Spearfish, South Dakota.

FIGS. *1, 2*—*Paraparchites?* sp. Interior and exterior views of a left valve, ×50. Loc. J-50b, 15 to 22 feet above base of member (USNM 106635). (p. 797)

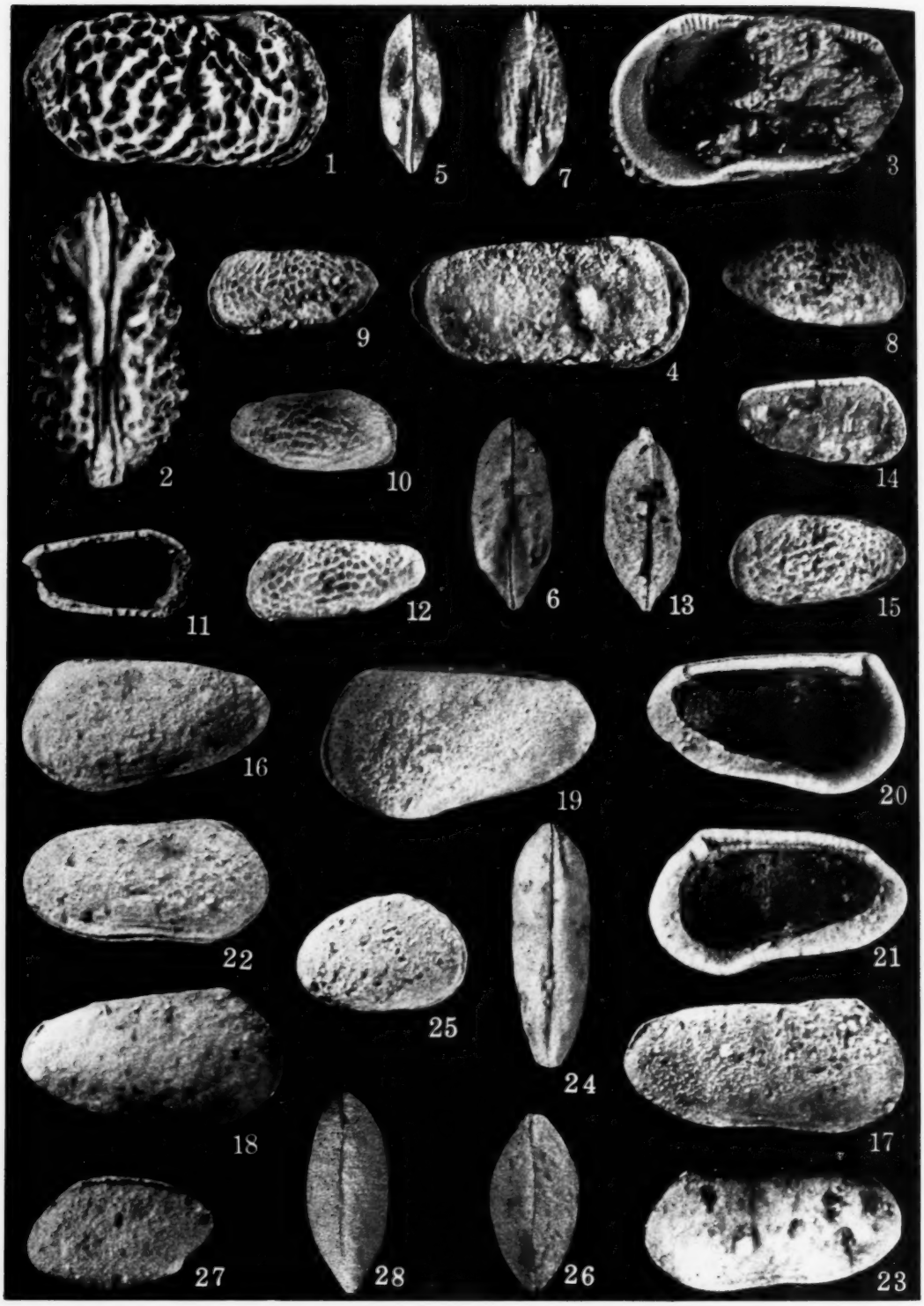
3–5—*Apatocythere? loeblichorum* Swain & Peterson, n. sp. *3*, Right side of holotype (USNM 106639). *4, 5*, Right side and interior views of two imperfectly preserved paratypes (USNM 106640, 106641), ×77. Loc. J-50k, 82 to 87 feet above base of member. (p. 799)

6–9—*Eridoconcha monopleura* Swain & Peterson, n. sp. *6, 9*, Dorsal and end views of a right valve paratype (USNM 106636). *7*, Interior view of left valve cotype (USNM 106638). *8*, Exterior view of right valve cotype (USNM 106637). ×68. Loc. J-50b, 15 to 22 feet above base of member. (p. 798)

10–18—*Progonocythere hieroglyphica* Swain & Peterson, n. sp. *12*, Right side of holotype (USNM 106642), loc. J-50f, 48 to 55 feet above base of member. *10, 11, 16*, Right sides of three paratypes (USNM 106646–106648), loc. J-50c, 22 to 33 feet above base of member. *15*, Interior of a paratype left valve (USNM 106650), loc. J-50d, 33 to 41 feet above base of member. *17*, Left side of a paratype (USNM 106649), loc. J-50e, 41 to 48 feet above base of member. *14*, Left side of a paratype (USNM 106644); *13, 18*, dorsal views of female and male paratypes (USNM 106643, 106645), loc. J-50f, 48 to 55 feet above base of member. All ×76. (p. 800)



Swain and Peterson, Upper Jurassic Ostracoda



Swain and Peterson, Upper Jurassic Ostracoda

bluntly acuminate slightly dorsad of mid-height, truncate above and below.

Left valve slightly larger than right, extending beyond the other along free margins. Convexity of presumed female dimorphs moderate, exceeding that of males; greatest thickness in posterior two-thirds of shell.

Ends compressed, provided with a knife-edged marginal rim. General surface of valves ornamented by strong ridges, consisting of two or three concentric but discontinuous outer ridges, four or five postmedian vertical ridges, and several diversely arranged anteromedian ridges. A short, oblique sulcus occurs near anterocardinal angle on each valve.

Hinge of left valve consists of terminal, elongate, weakly denticulate sockets, separated by an interterminal very weakly crenulate bar formed by the slightly extended valve edge; dorsal surface of interterminal bar slightly incised for reception of overlapping interterminal hinge feature of right valve. Hinge of right valve consists of terminal, elongate, narrow, crenulate dental areas; the intervening narrow valve edge overhangs a faintly crenulate rabbet-groove, for reception of corresponding hinge surface of left valve. Inner lamellae fairly broad; line of concrescence and inner margin nearly coincide. Muscle scar not observed.

Length of holotype, 0.59 mm.; height, 0.32 mm.; thickness, 0.27 mm.

Relationships.—The general shape, surface ornamentation and hingement of this species conform to characteristics prescribed for *Progonocythere* Sylvester-Bradley (1948). In its straight hinge, subquadrate outline, compressed ends, and reticulate surface, *Progonocythere*, particularly *P. hieroglyphica* is very close to *Loxoconcha* Sars. In that genus, however, there are terminal, rounded, knoblike teeth and circular sockets that are very different from the terminal hinge elements in *Progonocythere*. *P. blakeana* (Jones) as described by Sylvester-Bradley (1948, p. 191) from the Bathonian of England is related to the present species, but is more narrowly rounded posteriorly and has fewer

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EXPLANATION OF PLATE 114

Unless otherwise noted, all specimens are from the type locality of the Redwater shale member of the Sundance formation, about 7 miles northwest of Spearfish, South Dakota.

FIGS. *1–4*—*Progonocythere crowcreekensis* Swain & Peterson, n. sp. *1, 2*, Right side (×52) and dorsal view (×59) of cotypes (USNM 106651, 106652). Loc. J-50c, 22 to 33 feet above base of member. *3*, Interior of a paratype right valve (USNM 106653), ×61. Loc. J-50d, 33 to 41 feet above base of member. *4*, Right side of an abraded paratype (USNM 106654), ×59. Loc. J-50a, 5 to 15 feet above base of member. (p. 802)

5, 6, 27, 28—*Cytherura? lanceolata* Swain & Peterson, n. sp. *5, 6*, Ventral views of two paratypes (USNM 106655, 106656), ×75. *27, 28*, Left side and dorsal view of holotype (USNM 106657), ×75. Loc. J-50e, 41 to 48 feet above base of member. (p. 802)

7–15—*Monoceratina sundancensis* Swain & Peterson, n. sp. *8*, Right side view of a cotype (USNM 106658); *15*, left side view of a second cotype (USNM 106659); *7, 9*, ventral view and left side of two paratypes (USNM 106660, 106661); *12–14*, Left side, dorsal view, and poorly preserved left interior of three paratypes (USNM 106662–106664); ×75, loc. J-50c, 22 to 33 feet above base of member. *10, 11*, Right side and imperfectly preserved left interior of two paratypes (USNM 106665, 106666), ×75, loc. J-50d, 33 to 41 feet above base of member. (p. 803)

16–24—*Leptocythere imlayi* Swain & Peterson, n. sp. *16–18*, Left side of holotype, right side of female and male paratypes (USNM 106667–106669); loc. J-50f, 48 to 55 feet above base of member. *19–21*, Left side, left interior and right interior of three paratypes (USNM 106670–106672). These specimens are from 107 to 112 feet above base of Redwater shale, 2 miles south of Little Horn River in sec. 22, T. 58 N., R 89 W., Sheridan County, Wyoming (not the type locality), and are illustrated to show hinge features of this species. Crenulation along hinge in figure 21 is weaker than that illustrated. *22–24*, Right side, left side and dorsal view of a female paratype (USNM 106673); loc. J-50d, 33 to 41 feet above base of member. All ×80. (p. 804)

25, 26—Cytheridea sp. Right side and dorsal view (USNM 106674), ×76. Loc. J-50i, 68 to 75 feet above base of member. (p. 805)

and differently arranged surface ridges.

Occurrence.—Sample J-50b, c, d, e, f, 33 to 73 feet above base of Redwater shale. Holotype, USNM 106642; paratypes, USNM 106643, 106650.

PROGONOCYTHERE CROWCREEKENSIS
Swain & Peterson, n. sp.
Plate 114, figures 1–4

Shell subquadrate in lateral view; highest near anterior end; hinge margin nearly straight, about three-fourths of shell length, with broadly obtuse cardinal angles, ventral margin nearly straight, subparallel to dorsum, passing with sharp curvature into terminal margins; anterior margin broadly and nearly uniformly rounded; posterior margin slightly more narrowly rounded, extended medially. Valves subequal, the left slightly larger, extending slightly beyond the other at cardinal angles. Female (?) dimorphs relatively longer but about equal in height and convexity to males (?). Valves rather strongly convex, with greatest thickness in posterior third.

Anterior end compressed in a narrow zone that bears a low marginal, weakly nodose rim. Extended median portion of posterior end forms a narrow, compressed, slightly caudate process. A shallow, oblique sulcus lies near anterodorsal angle. A weak vertical sulcus occupies dorsal portion of valve, slightly antrad of midlength; near midheight this sulcus defines a small, more anterior, dorsoventrally elongate node. Ventral surface somewhat swollen, slightly overhangs ventral margin as viewed laterally. General surface of each valve coarsely reticulate.

Hinge of right valve as observed in one poorly preserved specimen, consists of an anterior crenulate, elongate, elevated dental area, and a posterior, elongate, crenulate, only slightly elevated dental area; interterminal portion formed by the slightly crenulate and weakly grooved valve edge. Hinge of left valve not observed. Inner lamella of right valve of moderate width, very finely and concentrically striated anteroventrally; line of concrescence and inner margin nearly coincide. Muscle scar not observed.

Length of female (?) cotype, 0.89 mm.; height, 0.45 mm.; thickness, 0.44 mm. Length of a male (?) cotype, 0.756 mm.; height, 0.45 mm.; thickness, 0.40 mm.

Relationships.—In general shape, rugose surface ornamentation and hingement this form is related to *P. hieroglyphica*, n. sp., but has a reticulate surface, rather than one with a series of more distinct and continuous ridges, and is a much larger form.

Occurrence.—Samples J-50 c, d, 40 to 59 feet above base of Redwater shale. Cotypes, USNM 106651, 106652; paratypes, USNM 106653, 106654.

Genus CYTHERURA Sars, 1865
CYTHERURA? LANCEOLATA
Swain & Peterson, n. sp.
Plate 114, figures 5, 6, 27, 28; text-fig. 1

Shell small, subovate-acuminate in side view; highest about one-third from anterior end; hinge margin slightly convex, about three-fifths of shell length, with well-defined but broadly obtuse cardinal angles; ventral margin gently convex, interrupted postventrally by overhanging short ala; anterior margin narrowly rounded, most extended just ventrad of midheight, truncate above; posterior margin acuminate, strongly extended and caudate dorsad of midheight. Valves nearly equal in size; right valve extends slightly beyond left along hinge, and left extends slightly beyond right along ventrum. Valves compressed; greatest thickness median to slightly postmedian.

General surface of valves smooth. Midventrally are low alate expansions that terminate in blunt points near postventral marginal bend; in posterior view, alae do not appreciably affect general convexity of valves, but provide a flattened and slightly overhanging ventral surface.

Edge of left valve along hinge apparently fits underneath edge of right without interlocking processes, but relationships are not completely understood owing to conditions of preservation. In the holotype, as viewed by transmitted light, inner lamellae moder-

ately broad; line of concrescence and inner margin separated; posteriorly, inner margin and line of concrescence slightly straightened, not following curvature of posterior margin. Muscle scar and pore canals not observed.

Length of holotype, 0.38 mm.; height, 0.22 mm.; thickness, 0.16 mm.

Relationships.—In general outline, produced posterior end and ventral alae, and in the simplicity of the hinge this species is related to *Cytherura* Sars. The hinge in *Cytherura* bears weak terminal teeth in the right valve and in the left there are weak teeth fitting in front of the anterior right valve tooth and behind the posterior right valve tooth (cf. Stephenson, 1946, p. 317). Lack of understanding of the details of the hinge in the present form prevents a definite comparison with *Cytherura* on the basis of hingement. Furthermore, the posterior portion of the inner lamellae of *Cytherura* are characteristically much broadened as a curved platform. In *C. lanceolata*, n. sp. this feature is missing, although there is minor widening of the posterior inner lamella, that results in a posterior straightening of the inner margin. In spite of this difference from typical *Cytherura*, the new species is believed to be more closely related to it than to such other alate forms as *Cytheropteron* Sars in which there is marked crenulation of the hinge surface, or *Brachycythere* Alexander in which there are prominent anterior knoblike teeth and sockets, posterior crenulate teeth and sockets and interterminal groove and bar. A general relationship of this species to *Paradoxostoma* Fischer and other genera of the Paradoxostominae Sars results from broadly sigmoidal outline of the margins of the dorsal and ventral halves of the shell, but alae have not been reported to occur in that subfamily.

Cytheridea trapezoidalis Terquem as illustrated and described by Jones and Sherborn (1888, p. 270, pl. 4, figs. 1a, b) is a somewhat similar species, but lacks pointed postventral alae and has a longer hinge.

Occurrence.—Samples J-50c, d, e, f, 40 to 73 feet above base of Redwater shale. Holotype, USNM 106657; paratypes, USNM 106655, 106656.

Genus MONOCERATINA Roth, 1928

MONOCERATINA SUNDANCENSIS
Swain & Peterson, n. sp.
Plate 114, figures 7–15; text-fig. 1

Shell small, subquadrate-acuminate in side view; highest about one-fifth from anterior end; hinge margin nearly straight, slightly sinuous, about four-fifths of shell length; ventral margin gently convex, converging strongly toward posterior with respect to dorsum; anterior margin broadly rounded, slightly extended below, subtruncate above; posterior margin narrowly rounded, bluntly acuminate, strongly extended above. Valves subequal, right extending slightly beyond left along hinge. Convexity of valves low; greatest thickness median.

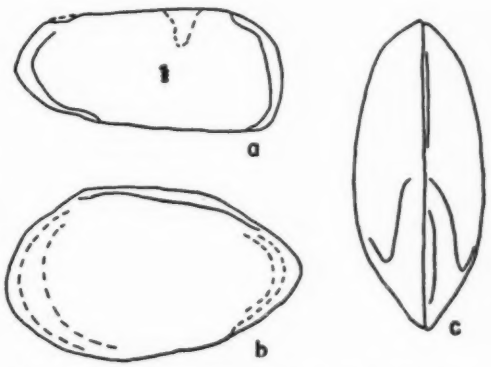

FIG. 1—Camera-lucida drawings, made by transmitted light.
a—Right view of a paratype of *Monoceratina sundancensis*, n. sp. (see pl. 114, fig. 10), showing adductor scar pattern and position of inner margin. True length, 0.34 mm.
b, *c*—Left and ventral outline views of holotype of *Cytherura? lanceolata*, n. sp. (see pl. 114, figs. 27, 28). In *b*, the inner dashed lines represent the inner margin, and the outer represent the line of concrescence. True length, 0.39 mm.

Median dorsal surface of each valve typically bears a shallow vertical sulcus that terminates at or dorsad of midheight; in some examples sulcus very weak or absent. Anterior end of shell compressed to form a narrow marginal rim. Posterior end com-

pressed to form a blunt caudate extension in dorsal half; compression continues ventrally and anteriorly to about one-third from posterior end. Ventral surface moderately swollen, near postventral marginal bend forms a low, rounded, slightly overhanging elevation. General surface of valves coarsely, but weakly reticulate, with depressions weakly pitted in some examples. Medially, some longitudinal elements of reticulum are slightly more elevated; in peripheral portion some concentric ridges are likewise slightly more pronounced than their neighbors.

Hinge of right valve consists of simple valve edge that evidently slightly overlaps corresponding edge of left; each valve bears obscure weak notches at both ends of hinge.

Inner lamellae of moderate width, sloping steeply toward valve interior; line of concrescence and inner margin slightly separated anteriorly. Radial canals not observed. Muscle scar as observed in one specimen consists of a vertical row of four elongate spots lying slightly antrad of midlength.

Relationships.—The outline, hingement, musculature and postventral swelling of this species indicate relationship to *Monoceratina* Roth, at least to Mesozoic and Cenozoic ostracodes that have been assigned to that genus. Several species that are generally similar to the present one have been described from the Lower and Middle Jurassic of Germany (Triebel and Bartenstein, 1938) and from the Middle Jurassic of England (Sylvester-Bradley, 1948).

The new species differs from *M. vulsa* (Jones & Sherborn), *M. scrobiculata* Triebel & Bartenstein, and *M. herburyensis* Sylvester-Bradley from the Middle Jurassic in its reticulate surface, as contrasted to the pitted surface of the other species. *M. amlingstadtensis* Triebel & Bartenstein from the Lias and *M. opalina* T. & B. from the Dogger of Germany have a different pattern of reticulation than *M. sundancensis*, and a different development of the postventral elevation of the valve.

The trivial name of this species is assigned on the basis of its known range throughout the Sundance formation at other localities in the western interior United States.

Occurrence.—Samples J-50c, d, 40 to 59 feet above base of Redwater shale. Cotypes, USNM 106658, 106659; paratypes, USNM 106660–106666.

Genus LEPTOCYTHERE Sars, 1925

Shell narrow, elongated, greatest height in anterior third; dorsal margin nearly straight; ventral margin sinuous, turned inward medially; anterior margin more broadly rounded, subtruncate above; posterior margin narrowly rounded, post-dorsal angle pronounced. Surface more or less faintly ornamented with pits, sometimes reticulate.

Hinge of left valve consists of an anterior socket and tooth, a posterior socket, and an interterminal groove below which lies a crenulate ridge. Inner lamellae moderately broad, especially in anterior end; pore canals moderately numerous.

Type species.—*Cythere pellucida* Baird.

Discussion.—Triebel (1941) figured two specimens from the Dogger of Europe which he questionably assigned to *Leptocythere*. These are very similar to those figured by Sars (1925) except for the more prominent posterodorsal angle of the latter's specimens. In the same paper, Triebel illustrated two views (taken from Brady) of *Leptocythere ? pavonia*, a Recent form, which differs from Sars' examples by its somewhat greater inflation and by the presence of three large, deep pits near the postventral margin.

LEPTOCYTHERE IMLAYI Swain & Peterson, n. sp.

Plate 114, figures 16–24

Shell elongate-subquadrate in lateral view; highest about one-fifth from anterior end; hinge margin nearly straight, about two thirds of shell length, with well defined only slightly obtuse anterocardinal angle and poorly defined broadly obtuse postcardinal angle; ventral margin sinuous, converging strongly toward posterior with respect to dorsum in female (?) dimorphs, less strongly in more elongate males (?); anterior

margin broadly rounded, slightly extended medially, subtruncate above; posterior margin narrowly rounded, most extended dorsad of midheight. Valves nearly equal in size; right extends slightly beyond left along hinge; left extends slightly beyond right along dorsal slopes. Valves not strongly convex; greatest thickness antrad of midlength.

Surface smooth except for scattered, widely spaced weak pits that mark positions of normal canals.

Hinge of left valve consists of a small anterior socket that opens ventrally into valve interior, a long interterminal, weakly and sparsely denticulate bar, slightly broadened at its anterior end, and a very small posterior socket. Hinge of right valve consists of a small anterior rounded tooth, an interterminal, very weakly and not completely denticulate groove, broadened at its anterior end for reception of corresponding bar in left valve, and a very small posterior tooth-like elevation formed by valve edge. Anteromedian portion of outer margin along ventrum in right valve strongly inturned and overlapped by left valve. Inner lamellae moderately broad; line of concrescence and inner margin only slightly separated. Radial canals few, widely spaced. Muscle scar consists of an anteromedian subvertical row of four small spots together with a single more anterior spot.

Length of holotype (pl. 114, fig. 16), 0.47 mm.; height, 0.256 mm.; thickness, 0.19 mm.

Relationships.—The elongate form, straight hinge, generally smooth surface, hingement and musculature of this species suggests comparison with *Leptocythere*, as described by Sars (1925) and van den Bold (1946). The most conspicuous difference from typical *Leptocythere* is the more pointed posterior end and resulting more obtuse postcardinal angle of the present species. These features typify the shorter more oblique dimorphs, whereas the longer ones are conspicuously less pointed posteriorly, but even in the latter, the differences in outline from described species are sufficient for recognition of a distinct species.

According to Sars (1928, pp. 172–176), the males in *Leptocythere* are more elongate and more tapering toward the posterior end than the females. In the present examples the shorter forms are the more tapering, but are also slightly more convex, so they are here considered tentatively as females.

This species apparently is one of the earliest known ostracodes characterized by anterior teeth and sockets, postjacent tooth-like elevation and depression and posterior weaker teeth and sockets. Except for surface ornamentation, a close relationship evidently exists between *Leptocythere imlayi* and species of *Buntonia* Howe (Howe and Chambers, 1935) as well as several species of "*Cythereis*" Jones as typified by "*C.*" *evergreenica* (Stadnichenko) (cf. Stephenson, 1946).

Leptocythere has not been previously reported as fossil, except for a questionable identification, *Leptocythere*? sp. by Triebel (1941, pl. 7), from the Middle Jurassic of Germany. Triebel's example is nearly identical to the present species in outline, but its surface bears very large normal canals.

Occurrence.—Samples J-50f, g, i, 66 to 93 feet above base of Redwater shale. Holotype, USNM 106667; paratypes, USNM 106668–106673.

Genus CYTHERIDEA Bosquet, 1850

CYTHERIDEA? sp.

Plate 114, figures 25, 26

Shell subovate in side view; highest about two-fifths from anterior end; dorsal margin strongly convex, sloping steeply antrad of position of greatest height, less steep behind, merging gradually with terminal margins; ventral margin slightly convex; anterior margin broadly rounded, slightly extended below; posterior margin more narrowly and more uniformly rounded. Left valve slightly larger, extending beyond right except midventrally. Valves moderately convex, greatest thickness postmedian and ventral.

Surface imperfectly preserved but apparently smooth.

Internal features not observed owing to recrystallization of matrix that fills shell.

Length of figured specimen, 0.33 mm.; height, 0.23 mm.; thickness, 0.18 mm.

Remarks.—In its ovate outline, narrowly rounded posterior end and curved dorsal margin this form is related to the general group of cytherideid ostracodes, particularly to *Haplocytheridea* Stephenson (1936). Lack of knowledge of the internal structures in the single specimen at hand prevents its definite identification.

Occurrence.—Sample J-50i, 86 to 93 feet above base of Redwater shale, USNM 106674.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, PP. 808–816, PLS. 115–117, 1 FIG., NOVEMBER 1951

THE OSTRACODE *CYTHERELLOIDEA* IN NORTH AMERICA

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ABSTRACT—The history of *Cytherelloidea* is reviewed. Five new species from the Upper Cretaceous and six from the Miocene of the Gulf Coast are described. All American species are figured and the stratigraphic positions of species known in the United States are shown in tables.

OSTRACODES now identified as *Cytherelloidea* first received attention under the generic name of *Cythere*, and later they were included in the subgenus *Cytherella* Jones, 1849. Sars (1865) after studying living specimens raised *Cytherella* to generic rank and proposed the suborder Platycopa to include all such Ostracoda. In ensuing years, most zoologists and paleontologists identified all ornate forms as *Cytherella williamsoniana*, a species described by Jones (1849) from the Lower Cretaceous.

Not until 1929 did the careful investigations by Alexander of the Cretaceous in North Texas show that *Cytherella* and *Cytherelloidea* are separate genera. He demonstrated that while the two share some characters, they are sufficiently distinct in others to warrant the erection of the new genus *Cytherelloidea*. This was followed by the recognition of numerous species throughout the world, and up to the present time, 91 species have been assigned to the genus, including the new species described here.

Several species described from the Dutch East Indies by LeRoy, Kingma, and others are ornamented differently from American and European forms; and possibly these should be excluded from *Cytherelloidea*.

All the previously described American species are listed and illustrated by reproductions of the original figures (pls. 115, 116).

DESCRIBED FROM NORTH AMERICA

RECENT

Cytherelloidea irregularis (Brady), 1880

PLEISTOCENE

Cytherelloidea californica LeRoy, 1943

MIOCENE

Cytherelloidea umbonata Edwards, 1944
C. moccasinensis Sexton, n. sp., 1951
C. anderseni Sexton, n. sp., 1951
C. purii Sexton, n. sp., 1951
C. blakei Sexton, n. sp., 1951
C. leonensis Howe, 1934
C. vernoni Sexton, n. sp., 1951
C. waynensis Sexton, n. sp., 1951

OLIGOCENE

C. byramensis Howe & Law, 1936
C. byramensis var. *conecuhensis* Howe & Law, 1936
C. castleberryensis Howe & Law, 1936
C. chawneri Howe & Law, 1936
C. murdercreekensis Howe & Law, 1936
C. rosefieldensis Howe & Law, 1936
C. vicksburgensis Howe, 1934
C. alabamensis Howe, 1934
C. hiwanneensis Howe, 1934

EOCENE

Jackson:
Cytherelloidea danvillensis Howe, 1934
C. ouachitensis Howe, 1934
C. montgomeryensis Howe, 1934
Claiborne:
C. smithvillensis Howe, 1934
Wilcox:
C. jessupensis Howe & Garrett, 1934
C. nanafaliensis Howe, 1934
C. tombigbeensis Howe, 1934
C. veatchiana Howe, 1934
C. truncata Schmidt, 1948
C. howei Swain, 1948

PALEOCENE (Midway)

Cytherelloidea tombigbeensis var. *delicata* Howe, 1934

UPPER CRETACEOUS

Cytherelloidea pecanana Sexton, n. sp., 1951
C. crafti Sexton, n. sp., 1951
C. tollettensis Sexton, n. sp., 1951
C. ozanana Sexton, n. sp., 1951
C. austinensis Sexton, n. sp., 1951
C. sp. Morrow, 1934
C. monmouthensis Jennings, 1936
C. navesinkensis Jennings, 1936
C. spiralia Jennings, 1936

LOWER CRETACEOUS

Cytherelloidea williamsoniana (Jones), 1849
C. obliquirugata Alexander, 1929
C. granulosa Alexander, 1929

C. reticulata Alexander, 1929
C. williamsoniana var. *stricta* Alexander, 1929
C. rhomboidalis Vanderpool, 1933
C. subgoodlandensis Vanderpool, 1933

JURASSIC

Cytherelloidea sp. Swain, 1949

Note: In addition to the tabulated species, Van den Bold (1949) has described *C. cubana* from Cuba, *C. olayensis* from Venezuela and *C. vaneeni* from Cuba and Guatemala, all Miocene. *C. bastropensis* Howe, 1934, was determined by Stephenson (1946), to be an immature molt of *C. smithvillensis*.

This study furnishes stratigraphically useful information because species of *Cytherelloidea* possess the constantly sought but seldom realized qualifications for "index or guide fossils": (1) they are distinctive, hence easily recognized; (2) they record definite morphological changes from one stratigraphic unit to another; and (3) they are numerous enough to be useful.

Additional undescribed species undoubtedly occur in the Upper Cretaceous and Tertiary. Several distinctively different single valves were found but the erection of new species on such specimens is inadvisable because the ornamentation is frequently different in the two valves.

Type specimens of the new species have been placed in the Henry V. Howe Collection, Louisiana State University, Baton Rouge, Louisiana.

Thanks are due Dr. Howe who supplied the materials on which the new species are based. The free use of his type collection and comprehensive library were indispensable aids in the preparation of this paper. Others who helped with suggestions are Dr. G. E. Murray and Mr. H. V. Andersen, both of the School of Geology, Louisiana State University.

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA Latreille
Suborder PLATYCOPA Sars
Family CYTHERELLIDAE Sars
Genus CYTHERELLOIDEA Alexander

Cythere (*Cytherella*) JONES, 1849, Palaeont. Soc. London, p. 31, pl. 7, fig. 26a–i.
Cytherella SARS, 1865 (1866), Vidensk selsk. Oslo (Christiania) Forh., pp. 124, 125.
Cytherelloidea ALEXANDER, 1929, Texas Univ. Bull. 2907, p. 55, pl. 2, fig. 12; VAN VEEN, 1932, Geol.-mijnb. genootsch. Nederland en Kolonien Verh., Geol. ser., D1, 9, p. 30; BONNEMA, 1940–1941, Natuurhist. Mannadbland, 27, 28, p. 95; LEROY, 1941, Jour. Paleontology, vol. 15, p. 612; EDWARDS, 1944, idem, vol. 18, p. 505; VAN DEN BOLD, 1946, Contribution to the study of Ostracoda with special reference to the Tertiary and Cretaceous microfauna of the Caribbean region, p. 20.

In side view oblong, oval, or subrectangular; greatest height commonly at anterior end. In dorsal view, greatest thickness posterior; width reduced anteriorly. Right valve slightly larger than the left; overlap apparent along venter and dorsum, not along entire periphery as in *Cytherella*. Valve interiors usually shallow; muscle pattern obscure, best seen in oil with transmitted light, consisting of two oblique rows of about seven scars each, as in *Cytherella*. Position of muscle scars marked by small protuberance normally at or just above valve center. Exterior with sulcus or muscle pit corresponding to interior protuberance. Hinge without teeth, articulation accomplished by a groove along dorsal margin of larger right valve and a sharp flange along the dorsal margin of left valve. Exterior surface always more or less ornamented by either a marginal rim, longitudinal ribs, pits, a sulcus, nodes, or any combination of these. Nodes or swellings on exterior have corresponding interior depressions. Ornamentation of two valves not uncommonly different.

The earliest reported occurrence of the genus is in sediments of Jurassic age in Europe and North America.

Genotype.—*Cythere* (*Cytherella*) *williamsoniana* Jones 1849, designated by Alexander, 1929.

CYTHERELLOIDEA AUSTINENSIS Sexton, n. sp.
Plate 117, figures 1, 2

Minute, subrectangular in side view, dorsal and ventral margins nearly straight. Anterior and posterior ends bluntly rounded. In dorsal view, much thickest posteriorly. Ornamentation of valves unlike. Left valve bears two ball-like knobs on posterior end, one above ventral margin, the other at posterodorsal angle. A sharply raised rim outlines anterior and extends back along dorsal margin almost to its center before dying out and, with height reduced, along ventral edge to the lower knob. A sharp, thread-like, arcuate rib extends above ventral rim from

CYTHERELLOIDEA IN NORTH AMERICA

	Claiborne Eocene, Texas	Moodys Branch, Lower Jackson, La.	Danville Landing, U. Jackson of La.	Red Bluff Oligocene, Mississippi	Byram Oligocene, Mississippi	Oligocene, Louisiana	Oligocene, Mississippi-Ala.	Oligocene, Alabama	Oligocene, Mississippi-La.	Chickasawhay Miocene, Oligocene, Miss.	Chipola, Miocene Florida	Choctawhatchee Miocene, Florida	*Ecphora* zone, Miocene, Florida	*Cancellaria-Pecten* zone, Miocene, Fla.	Duplin marl Miocene, North Carolina	Lomita marl, Pleistocene, Calif.	Recent
C. irregularis (Brady), 1880	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx
C. californica LeRoy, 1943	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx	
C. umbonata Edwards, 1944	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx		
C. anderseni Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx			
C. moccasinensis Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx			
C. purii Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx			
C. blakei Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx				
C. leonensis Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx					
C. vernoni Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx						
C. waynensis Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx							
C. byramensis Howe & Law, 1936	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx								
C. chawneri Howe & Law	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx								
C. byramensis conecuhensis Howe & Law, 1936	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx									
C. alabamensis Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx									
C. castleberryensis Howe & Law, 1936	. . .	. . .	. . .	. . .	. . .	. . .	xxx										
C. murdercreekensis Howe & Law, 1936	. . .	. . .	. . .	. . .	. . .	. . .	xxx										
C. rosefieldensis Howe & Law, 1936	. . .	. . .	. . .	. . .	. . .	xxx											
C. vicksburgensis Howe, 1934	. . .	. . .	. . .	. . .	xxx												
C. hiwanneensis Howe, 1934	. . .	. . .	. . .	xxx													
C. danvillensis Howe, 1934	. . .	. . .	xxx														
C. ouachitaensis Howe, 1934	. . .	. . .	xxx														
C. montgomeryensis Howe, 1934	. . .	xxx															
C. smithvillensis Howe, 1934	xxx																

CYTHERELLOIDEA IN NORTH AMERICA

	Schuler fm., Jurassic, La.	Paluxy fm., L. Cret., Okla.	Lower Cretaceous of Oklahoma	Ft. Worth fm., L. Cret., Texas	Denton fm., L. Cret., Texas	Weno formation, L. Cret., Texas	Grayson fm., L. Cret., Texas	Marshalltown fm., U. Cret., N. J.	Mt. Laurel fm., U. Cret., Dela.	Navesink fm., U. Cret., N. J.	Greenhorn fm., U. Cret., Kansas	Austin chalk, U. Cret., Texas	Ozan formation, U. Cret., Ark.	Marlbrook fm., U. Cret., Ark.	Pecan Gap fm., U. Cret., Texas	Midway Paleocene, Alabama	Eocene, Maryland	Aquia fm., Eocene, Va. and Maryland	Nanafalia fm., Wilcox Eocene, Ala.	Wilcox Eocene, Louisiana
C. jessupensis Howe & Garrett, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx
C. nanafaliensis Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx	xxx
C. tombigbeensis Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx
C. veatchiana Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx	
C. truncata Schmidt, 1948	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx		
howei Swain, 1948	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx			
C. tombigbeensis var. *delicata* Howe, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx				
C. pecana Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx					
C. crafti Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx						
C. tollettensis Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx							
C. ozanana Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx								
C. austinensis Sexton, n. sp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx									
C. sp. Morrow, 1934	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx	xxx										
C. monmouthensis Jennings, 1936	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx										
C. navesinkensis Jennings, 1936	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx	xxx	xxx										
C. spiralia Jennings, 1936	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx											
C. williamsoniana (Jones), 1849	. . .	. . .	. . .	. . .	. . .	. . .	. . .	xxx												
C. obliquirugata Alexander, 1929	. . .	. . .	. . .	. . .	. . .	. . .	xxx													
C. granulosa Alexander, 1929	. . .	. . .	. . .	. . .	. . .	xxx	xxx													
C. reticulata Alexander, 1929	. . .	. . .	. . .	xxx	xxx	xxx														
C. williamsoniana var. *stricta* Alex., 1929	. . .	. . .	xxx	xxx																
C. rhomboidalis Vanderpool, 1933	. . .	. . .	xxx																	
C. subgoodlandensis Vanderpool, 1933	. . .	xxx																		
C. sp. Swain, 1949	xxx																			

just above antero-ventral juncture back almost to lower posterior knob. A nearly straight rib extends forward from the upper node below dorsal margin but does not reach anterior rim. Muscle pit small and deep, below upper rib and above valve center. Right valve with marginal rim nearly continuous around ventral, anterior and dorsal edges, highest anteriorly. Posterior nodes almost undeveloped on right valve. From position of lower node, an obscure, slightly arcuate rib extends forward above ventral margin. A second rib is slightly indicated below dorsal margin, curving upward above the deep muscle pit.

Dimensions.—Length, 0.60 mm.; height, 0.31 mm.

Locality and Horizon.—Collected just north of bridge over Little Walnut Creek on the Austin-Manor road, Williamson County, Texas, from Austin chalk (Upper Cretaceous).

CYTHERELLOIDEA OZANANA Sexton, n. sp.
Plate 117, figures 4, 5

In side view subrectangular; ventral and dorsal margins almost parallel, straight; valves slightly higher posteriorly. In dorsal view, greatest thickness at posterior end. Anterior end evenly rounded; posterior rounded but subtruncate.

Young molts ornamented with a high raised rim around posterior, continuing as a low rim along ventral margin, becoming higher anteriorly, obsolescent dorsally. Adults with rim much higher and more pronounced posteriorly. A lower, nearly straight rib extends anteriorly just above ventral margin. A rather strong upper rib extends obliquely downward from near posterior dorsal corner toward the large, shallow, subcentral muscle pit, where it becomes very weak and bends sharply downward beneath pit and then upward again, dying out before reaching anterior rim. Right valve with a faint indication of a short longitudinal rib just above muscle pit extending almost to anterior rim.

Dimensions.—Length, 0.54 mm.; height, 0.28 mm.

Locality and Horizon.—Ozan formation, lower Taylor group (Upper Cretaceous), NE¼ sec. 33, T. 10 S., R. 27 W., Arkansas. Species based on one complete carapace, two adult right valves, and one immature right valve.

CYTHERELLOIDEA TOLLETTENSIS
Sexton, n. sp.
Plate 117, figures 3, 6

In side view subovate, ventral margin straight, dorsum very gently arched, greatest height central. In ventral view almost equally thick at ends and near middle,

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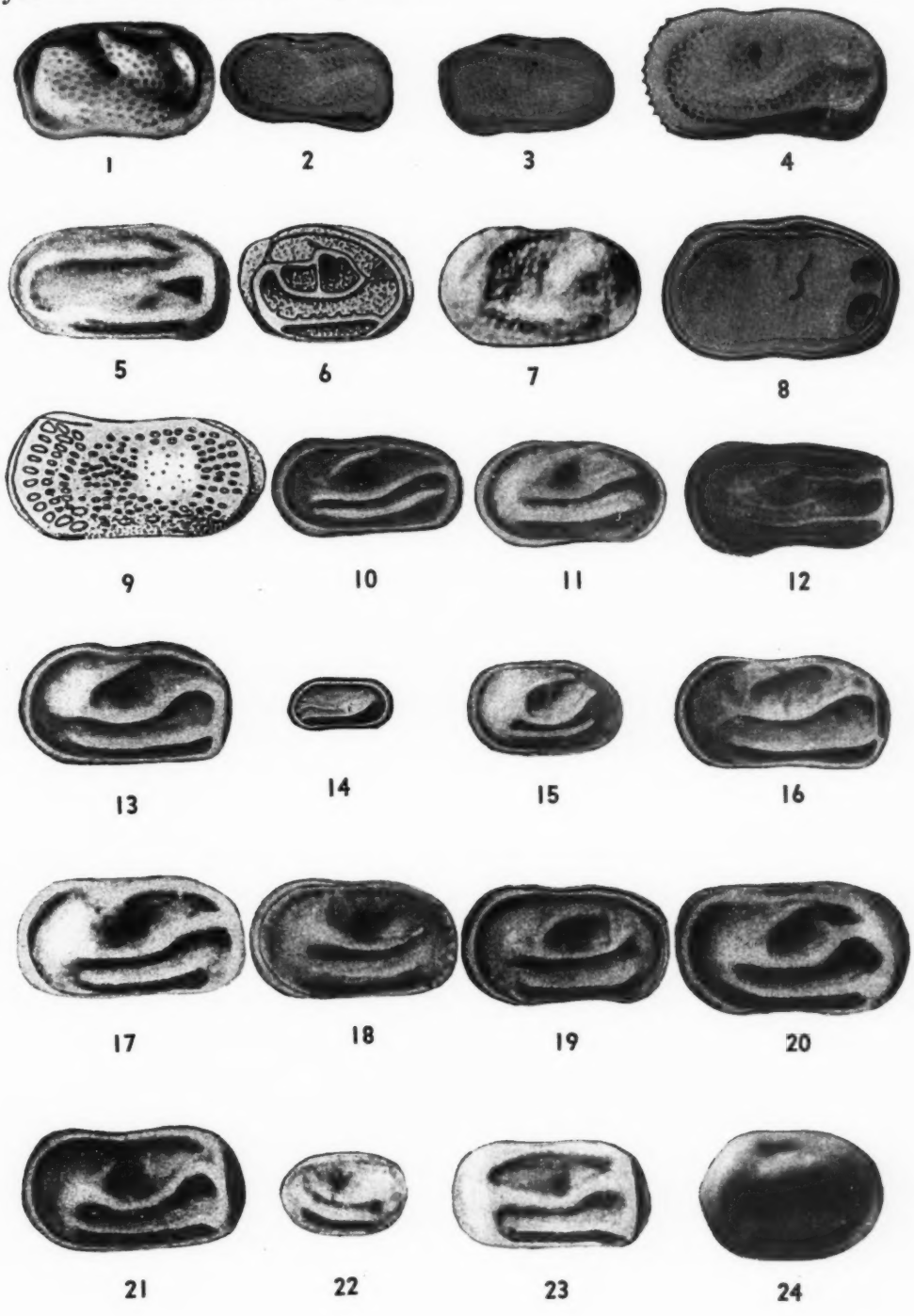
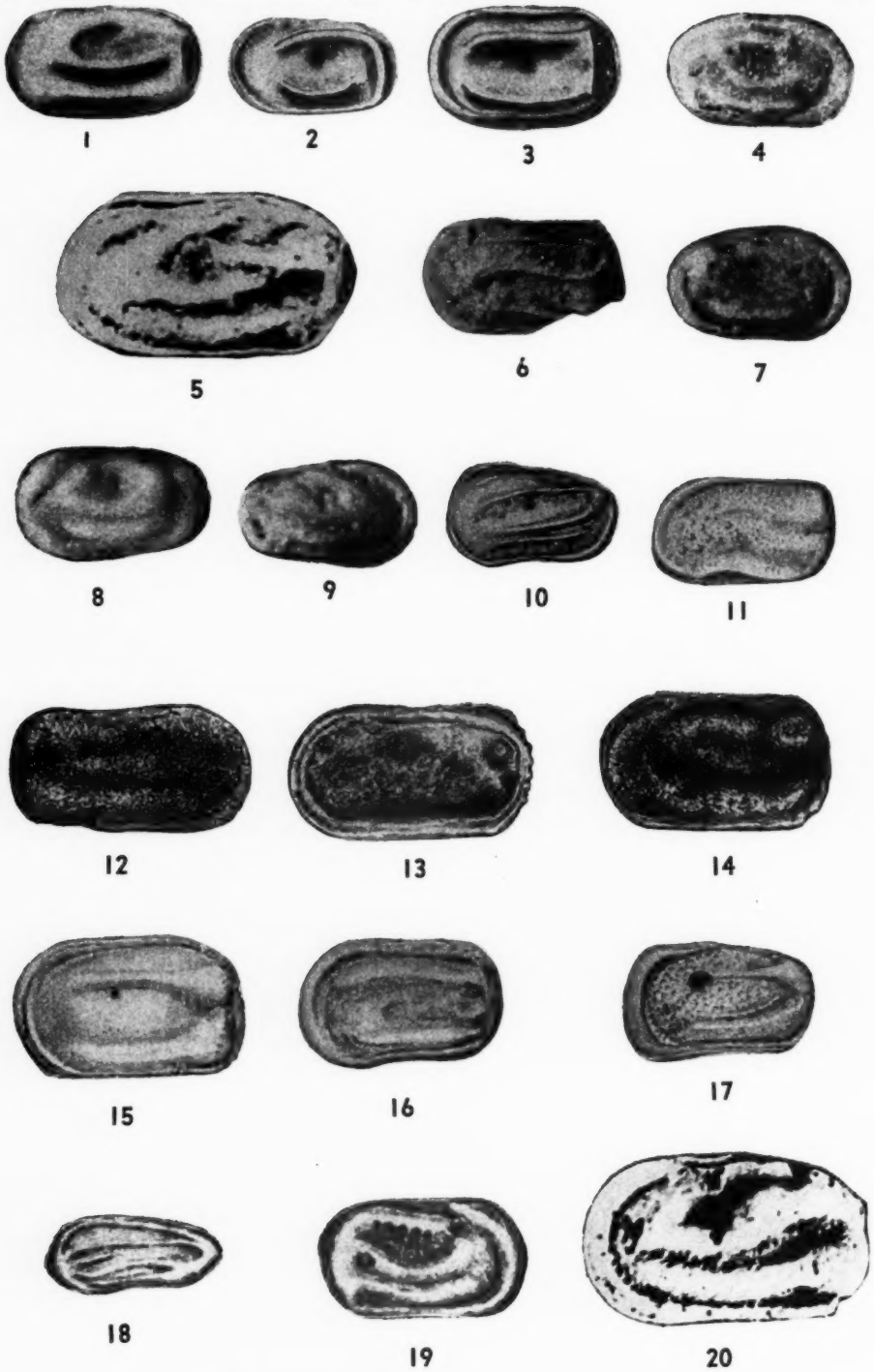
EXPLANATION OF PLATE 115

Reproduced from original illustrations. All figures approximately ×50.

FIG. *1*—*Cytherelloidea irregularis* (Brady). Right valve.
2, 3—*Cytherelloidea californica* LeRoy. *2*, Left valve; *3*, right valve.
4, 8—*Cytherelloidea umbonata* Edwards. *4*, Left valve exterior; *5*, right valve interior.
5—*Cytherelloidea leonensis* Howe. Left valve.
6—*Cytherelloidea cubana* van den Bold. Right valve.
7—*Cytherelloidea olayensis* van den Bold. Left valve.
9—*Cytherelloidea vanveeni* van den Bold. Left valve.
10—*Cytherelloidea byramensis* Howe & Law. Left valve.
11—*Cytherelloidea byramensis* var. *conecuhensis* Howe & Law. Left valve.
12—*Cytherelloidea castleberryensis* Howe & Law. Left valve.
13—*Cytherelloidea chawneri* Howe & Law. Left valve.
14—*Cytherelloidea murdercreekensis* Howe & Law. Left valve.
15—*Cytherelloidea rosefieldensis* Howe & Law. Left valve.
16—*Cytherelloidea vicksburgensis* Howe. Left valve.
17—*Cytherelloidea alabamensis* Howe. Left valve.
18—*Cytherelloidea hiwanneensis* Howe. Left valve.
19—*Cytherelloidea danvillensis* Howe. Left valve.
20—*Cytherelloidea ouachitensis* Howe. Left valve.
21—*Cytherelloidea montgomeryensis* Howe. Left valve.
22—*Cytherelloidea bastropensis* Howe. Left valve.
23—*Cytherelloidea smithvillensis* Howe. Left valve
24—*Cytherelloidea jessupensis* Howe & Garrett. Right valve.



Sexton, North American Cytherelloidea



Sexton, North American Cytherelloidea

narrower between. Dorsum appears thickest posteriorly, both ends truncate. Anterior end evenly rounded, marked by a sharp rim which extends backward along dorsal margin almost to posterior end. Posterior end rounded. Two prominent posterior nodes or swellings, one above the other, connected by a posteriorly-convex ridge. Upper node near posterodorsal juncture, continuing as a straight rib which extends anteriorly just below dorsal margin, terminating in advance of valve center. A lower thicker rib gently convex downward present just above ventral margin, forward extent about equal to upper rib; does not reach the lower node posteriorly. A small circular sulcus present just above valve center, nearer upper rib than lower.

This species resembles *C. pecana*, n. sp., in general appearance, but differs in the presence of the two prominent swellings and in its more oval shape. It is based on one complete carapace and one adult right valve.

Dimensions.—Length, 0.61 mm.; height, 0.39 mm.

Locality and Horizon.—Ozan formation, lower Taylor group (Upper Cretaceous), about 2 miles northeast of Tollette, Howard County, Arkansas.

CYTHERELLOIDEA CRAFTI Sexton, n. sp.
Plate 117, figures 7–10

In side view oblong, subrectangular; dorsal and ventral margins nearly straight. Anterior broadly rounded, posterior subtruncate. In dorsal view, strongly truncated and thickest posteriorly, also tapers anteriorly and marginal rims on both valves give truncate appearance. Right valve shaped differently from left, less elongate, with straighter dorsal margin. Surface ornamented with high, rounded anterior rim and posterior knob-like swellings continuing anteriorly as ribs. Lower rib of left valve slightly arcuate, almost fails to meet knob. The upper ribs of both valves bifurcate and pass around muscle pits. All ribs die out before reaching anterior rim. Interior of valves comparatively shallow. Right valve with continuous groove for reception of sharp edge of the left.

Young molts with much lower posterior nodes, three ribs instead of two. Ventral rib arcuate as in the adult, clearly joins lower node. Middle rib just below muscle pit, does not join upper rib. Upper rib extends from posterior swelling to upper edge of muscle pit where it dies out.

This species is based on one complete carapace, three adult left valves, one adult right valve, and ten immature valves. It is named for B. C. Craft, collector of the sample and Chairman of the Department of Petroleum Engineering at Louisiana State University.

Dimensions.—Length, 0.68 mm.; height, 0.41 mm.

Locality and Horizon.—Marlbrook forma-

EXPLANATION OF PLATE 116

Reproduced from original illustrations. All figures approximately ×50.

FIG. *1*—*Cytherelloidea nanafaliensis* Howe. Left valve.
2—*Cytherelloidea tombigbeensis* Howe. Left valve.
3—*Cytherelloidea veatchiana* Howe. Left valve.
4—*Cytherelloidea truncata* Schmidt. Right valve.
5—*Cytherelloidea howei* Swain. Right valve.
6—*Cytherelloidea* sp. Morrow. Left valve.
7—*Cytherelloidea monmouthensis* Jennings. Right valve.
8—*Cytherelloidea navesinkensis* Jennings. Right valve.
9—*Cytherelloidea spiralia* Jennings. Right valve.
10—*Cytherelloidea obliquirugata* (Jones & Hinde). Left valve.
11—*Cytherelloidea granulosa* (Jones). Left valve.
12—*Cytherelloidea williamsoniana* (Jones). Right valve.
13—*Cytherelloidea williamsoniana* (Jones). Interior of right valve.
14—*Cytherelloidea williamsoniana* (Jones). Left valve.
15—*Cytherelloidea williamsoniana* (Jones). Left valve.
16—*Cytherelloidea williamsoniana* var. *stricta* (Jones & Hinde). Left valve.
17—*Cytherelloidea reticulata* Alexander. Left valve.
18—*Cytherelloidea rhomboidalis* Vanderpool. Left valve.
19—*Cytherelloidea subgoodlandensis* Vanderpool. Right valve.
20—*Cytherelloidea* sp. Swain. Left valve.

tion, Taylor group (Upper Cretaceous), southeast corner sec. 29, T. 11 S., R. 27 W., Arkansas.

CYTHERELLOIDEA PECANANA Sexton, n. sp.
Plate 117 figure 11

In side view subquadrate, dorsal margin gently arched, venter almost straight, greatest height on anterior, tapering posteriorly. A high, sharp rim present all along margin except for short distance posteriorly, strongest anteriorly. Two thick, slightly sinuous ribs occur posteriorly, lower starts just above and in front of posteroventral angle, extends close above ventral margin, upper arises from a small swelling just inward from posterodorsal juncture, curves slightly up and around a large circular sulcus situated slightly posterior to and above valve center. Both ribs die out anterior to muscle pit. Ornamentation of valves similar but ribs of left thinner and muscle pit less well defined than in right.

Dimensions.—Length, 0.39 mm.; height, 0.23 mm.

Locality and Horizon.—Pecan Gap chalk Taylor group (Upper Cretaceous), 1 mile west of Taylor, on the Austin-Taylor highway, Williamson County, Texas.

CYTHERELLOIDEA WAYNENSIS Sexton, n. sp.
Plate 117, figure 12

In side view elongate, subrectangular. Dorsal margin with an inconspicuous hump posterior to middle, ventral indented at center. Anterior end evenly rounded, posterior slightly angular, truncate. Height uniform except at dorsal hump. In dorsal view slightly thickest posteriorly. Overlap evident just forward of dorsal hump. A low rim outlines anterior margin, continues less strongly along dorsal and ventral edges, becomes slightly higher posteriorly. Two rounded ribs begin at posterior rim, nearly parallel each other for most of valve length, lower terminates just short of antero-ventral angle, the other ends just above. Muscle area an indefinite depression near valve center above second rib.

Dimensions.—Length, 0.59 mm.; height, 0.37 mm.

Locality and Horizon.—Chickasawhay formation (Mio-Oligocene), NE¼ SW¼ sec. 10, T. 8 N., R. 7 W., Wayne County, Mississippi.

CYTHERELLOIDEA VERNONI Sexton, n. sp.
Plate 117 figure 13

In side view oblong, subrectangular, ventral and dorsal margins nearly straight, parallel, greatest height posterior to valve center. In dorsal view thickest posteriorly, thinning abruptly anteriorly, posterior truncate. Periphery outlined by broad flattened rim, highest posteriorly. A rib extends forward from posterior margin, curving slightly down and around a shallow, inconspicuous, subcentral muscle pit, dying out before reaching anterior rim. Sculpture similar in both valves but in right the marginal rim less distinct except posteriorly, rib slightly more arcuate than that on left valve.

This species is similar to *C. smithvillensis* Howe, except that its rib does not extend the entire length of the carapace. It is based on four complete specimens.

Dimensions.—Length, 0.64 mm.; height, 0.37 mm.; thickness, 0.28 mm.

Locality and Horizon.—Chipola formation (Miocene), NE¼ NE¼ sec. 20, T. 1 N., R. 16 W., Washington County, Florida. Collected by R. O. Vernon, Florida Geological Survey.

CYTHERELLOIDEA MOCCASINENSIS
Sexton, n. sp.
Plate 117, figure 14

In side view oblong-ovate, dorsal margin very slightly arched, ventral margin straight. Anterior end broadly rounded, capped by low flat rim following dorsum to posterodorsal margin where it becomes obscure. Rather prominent sulcus just above and slightly posterior to valve center, bumps rise above general surface anterior and posterior to the sulcus, one more prominent. Under posterior bump an elongated swelling extends forward between venter and sulcus for about one-half of valve length, obscuring rim on posterior and ventral margins. Valves translucent except for bumps and swellings.

This species resembles *C. irregularis* (Brady) but lacks its pitted surface.

Dimensions.—Length, 0.56 mm.; height, 0.32 mm.

Locality and Horizon.—*Cancellaria* zone (Miocene), NE¼ sec. 16, T. 1 S., R. 13 W.,

on Moccasin Creek beneath bridge, Bay County, Florida.

CYTHERELLOIDEA BLAKEI Sexton, n. sp.
Plate 117, figure 15

In side view oblong, subquadrate, dorsal margin gently arched, with slight hump just posterior to center, ventral margin with pronounced central indentation. Anterior end broadly, evenly rounded; posterior more angular, slightly oblique, subtruncate. Greatest height near anterior. In dorsal view, width slightly greater in posterior one-third. Overlap, right over left valve, apparent anterior to dorsal hump. Surface ornamented with weak ribs. A very faint, low rim present all around periphery, nowhere very pronounced. A low arcuate rib begins just above and behind posteroventral juncture, extends forward just above ventral margin, joins marginal rim at anteroventral angle, separated from ventral rim by narrow furrow. A second rib begins just below posterodorsal angle, connected to lower rib by a rather strong transverse bar, extends only a short distance before dying out near posterior side of small shallow sulcus located just above valve center. A weak, inconspicuous rib rises just in advance of sulcus, passes over it, curves upward and joins dorsal margin near hump.

The ornamentation of the two valves is essentially the same, and is not prominent in either. The upper, sinuous rib is particularly difficult to discern without meticulous inspection. This species is named in honor and memory of Daniel B. Blake.

Dimensions.—Length, 0.74 mm.; height 0.41 mm.

Locality and Horizon.—*Ecphora* zone of Choctawhatchee Miocene, Jackson Bluff, Leon County, Florida.

CYTHERELLOIDEA PURII Sexton, n. sp.
Plate 117, figure 16

In side view oblong, subrectangular; dorsal margin almost straight, but slightly concave just forward of center; ventral margin similarly concave just posterior to center. Anterior end slightly higher than posterior, evenly rounded, with raised rim which continues less strongly around remainder of periphery, slightly below valve margin on dorsum. Posterior end shorter, somewhat more angular. Thickest posteriorly. A rib originating at posteroventral angle extends just above ventral margin to anteroventral juncture; another begins just below posterodorsal margin, well defined for less than one-half of valve length; a poorly defined third rib forms simple arc to point just before and above termination of lower rib. Area inside peripheral rim and between ribs slightly pitted.

This species most closely resembles *C. anderseni*, n. sp., but differs in that the rib just above the ventral margin joins the anterior rim, and the surface pits are less prominent. It is named for Harbans S. Puri of Calcutta, India.

Dimensions.—Length 0.53 mm.; height 0.30 mm.; thickness 0.19 mm.

Locality and Horizon.—Uppermost part of section at Jackson Bluff, the *Pecten* bed (Miocene), Leon County, Florida. Sample collected by H. V. Howe.

CYTHERELLOIDEA ANDERSENI Sexton, n. sp.
Plate 117, figure 17

Almost rectangular in side view; center of dorsal margin concave; ventral margin similarly concave more posteriorly. Anterior end broadly rounded, constituting highest part of carapace, posterior end oblique. Valve overlap, right over left, on dorsal and ventral margins. A rim outlines valve margins, most prominent dorsally and posteriorly. A rib originating at posterior margin extends just above ventral rim for about two-thirds of valve length. A second rib begins just below posterodorsal juncture, strongly developed for about one-third of valve length, becomes less distinct, bends sharply under shallow sulcus, ends in a very slight swelling anterior to valve center and above termination of lower rib. Surface coarsely pitted and hyaline except for ribs and most of area between them.

This species is named for Mr. Harold V. Andersen, Instructor of Micropaleontology at Louisiana State University.

Dimensions.—Length, 0.61 mm.; height, 0.33 mm.; thickness, 0.18 mm.

Locality and Horizon.—Chipola formation (Miocene), NE¼ NE¼ sec. 20, T. 1 N., R. 16 W., Washington County, Florida. Collected by R. O. Vernon, Florida Geological Survey.

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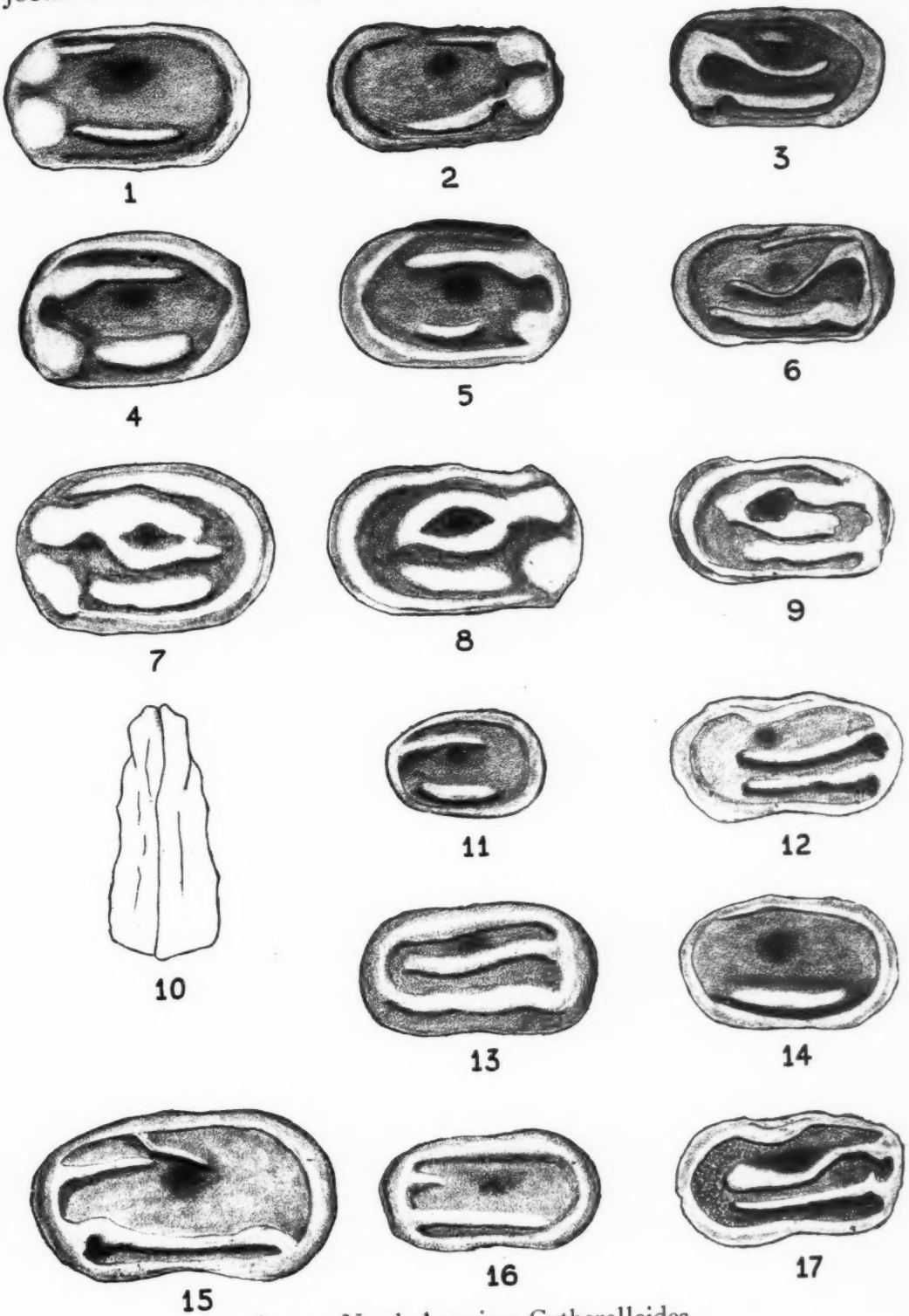
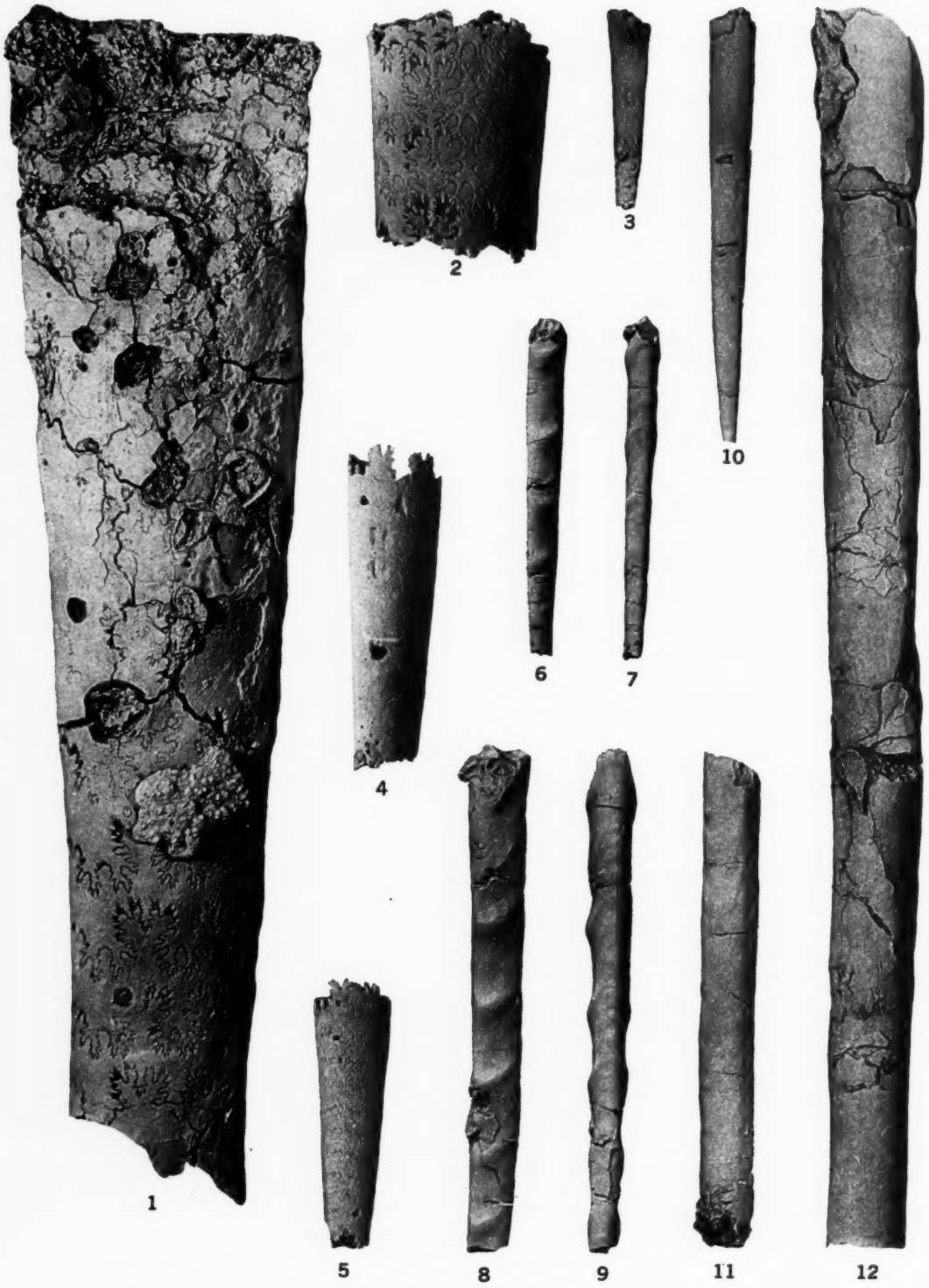
EXPLANATION OF PLATE 117

All figures approximately ×50.

FIGS. *1, 2*—*Cytherelloidea austinensis* Sexton, n. sp. *1*, Right valve; *2*, left valve. (p. 809)
3, 6—*Cytherelloidea tollettensis* Sexton, n. sp. *3*, Right valve; *6*, left valve. (p. 812)
4, 5—*Cytherelloidea ozanana* Sexton, n. sp. *4*, Right valve; *5*, left valve. (p. 812)
7–10—*Cytherelloidea crafti* Sexton, n. sp. *7*, Right valve; *8*, left valve; *9*, immature molt of left valve; *10*, dorsal view. (p. 813)
11—*Cytherelloidea pecanana* Sexton, n. sp. Right valve. (p. 814)
12—*Cytherelloidea waynensis* Sexton, n. sp. Left valve. (p. 814)
13—*Cytherelloidea vernoni* Sexton, n. sp. Left valve. (p. 814)
14—*Cytherelloidea moccasinensis* Sexton, n. sp. Right valve. (p. 814)
15—*Cytherelloidea blakei* Sexton, n. sp. Right valve. (p. 815)
16—*Cytherelloidea purii* Sexton, n. sp. Right valve. (p. 815)
17—*Cytherelloidea anderseni* Sexton, n. sp. Left valve. (p. 815)



Sexton, North American Cytherelloidea



Cobban, Cretaceous *Baculites*

JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, PP. 817–821, PL. 118, 13 TEXT FIGS., NOVEMBER 1951

NEW SPECIES OF *BACULITES* FROM THE UPPER CRETACEOUS OF MONTANA AND SOUTH DAKOTA[1]

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ABSTRACT—*Baculites mariasensis*, *B. sweetgrassensis* and *B. gregoryensis* are described as new. The first two are of Niobrara age, and the last is from rocks of Judith River age. The baculite zones of the northern Great Plains are reviewed.

MANY collections of fossils from the Upper Cretaceous rocks of the western interior United States contain several undescribed species of baculites that are of value in correlation. Two new species, *Baculites mariasensis* and *B. sweetgrassensis*, occur in shale and sandstone equivalents of the Fort Hays limestone member of the Niobrara formation. *B. gregoryensis*, n. sp., occurs in marine rocks equivalent to the Judith River formation of central Montana. The recognition of these species makes it possible to construct a more complete Upper Cretaceous time scale for the Western Interior based on *Baculites*. The zones constitute the following sequence in the northern Great Plains.

Montana age	*B. grandis*
	B. compressus
	B. gregoryensis
	B. asperiformis
	B. aquilaensis
Colorado age	*B. thomi*
	B. codyensis
	B. mariasensis
	B. cf. *besairiei*
	B. gracilis

Baculites gracilis Shumard characterizes the Greenhorn limestone of the Black Hills and the equivalent calcareous beds in the middle of the Colorado shale of north-central Montana. *Baculites* cf. *besairiei* Collignon occurs in the Carlile shale of the Black Hills and in the equivalent part of the Colorado shale of Montana. *B. mariasensis*, n. sp., is present in the upper part of the Colorado shale of Montana and in the upper part of the Frontier formation of west-central Wyoming. *B. codyensis* Reeside, of upper Niobrara age, is abundant in the Cody shale of Wyoming and in the upper part of the Colorado shale of Montana (above the zone of *B. mariasensis*). *B. thomi* Reeside occurs in the uppermost part of the Colorado shale of north-central Montana and in the Telegraph Creek formation of north-central and south-central Montana. *B. aquilaensis* Reeside characterizes the Eagle sandstone of Montana, the Gammon ferruginous member of the Pierre shale of the Black Hills, and parts of the Steele and Cody shales of Wyoming. *B. asperiformis* Meek is the most common form in the Claggett shale of Montana and in the Mitten black shale member of the Pierre shale of the Black Hills. *B. gregoryensis*, n. sp., occurs in the calcareous Gregory member of the Pierre shale in the Missouri Valley of South Dakota, and in a 200-foot sandy shale member of the Pierre

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EXPLANATION OF PLATE 118

All figures natural size.

FIGS. *1–5*—*Baculites gregoryensis* Cobban, n. sp. *1*, Lateral view of holotype; *2–5*, lateral views of four paratypes. Gregory member of Pierre shale, 2 miles west of Oacoma, Lyman County, South Dakota. (p. 820)

6–9—*Baculites sweetgrassensis* Cobban, n. sp. *6*, *7*, Lateral and ventral views of paratype; *8*, *9*, lateral and ventral views of holotype. Colorado shale, 5.5 miles south of Shelby, Toole County, Montana. (p. 820)

10–12—*Baculites mariasensis* Cobban, n. sp. *10*, *11*, Lateral views of paratypes; *12*, lateral view of holotype. Colorado shale, 5.5 miles south of Shelby, Toole County, Montana. (p. 818)

shale immediately overlying the Mitten black shale member in the Black Hills. *B. compressus* Say is present through most of the Bearpaw shale of Montana, through much of the upper part of the Pierre shale of the Black Hills (above the beds containing *B. gregoryensis*), and in that part of the Pierre shale between the Gregory and Mobridge members of the Missouri Valley of South Dakota. *B. grandis* Hall & Meek marks the uppermost Bearpaw shale of Montana, the uppermost Pierre shale of the Black Hills (above the Monument Hill bentonitic member), and the Mobridge member of the Pierre shale of the Missouri Valley of South Dakota.

Types of the new species are deposited in the United States National Museum, Washington. The photographs were made by Nelson A. Shupe, United States Geological Survey.

BACULITES MARIASENSIS Cobban, n. sp.
Plate 118, figures 10–12; text-figures 4–7

Shell small with scarcely any taper beyond the early stages; cross-section broadly eliptical below a diameter of 2 or 3 mm., more compressed between diameters of 3 to 5 mm., and ovate with narrow venter at all greater diameters. Dorsum and flanks smooth although an occasional individual may show scarcely perceptible lateral ribs. Venter smooth in early stages; ribbed beyond diameters of 6 to 8 mm. The ventral ribs, which are closely spaced, curve back sharply after crossing the venter and disappear on the lower part of the flanks. The holotype, which is almost one-half living chamber, attains a maximum diameter of about 16 mm.

The suture is relatively simple with narrow lobes and broad subequal saddles.

Remarks.—This species is characterized by its near lack of taper, oval cross-section with narrow venter, smooth shell, and simple suture. It is a fairly small shell, the largest septate fragment examined being 21 mm. in diameter. The nearest described American species is *Baculites gracilis* Shumard as figured by Stanton (1893). That species, however, has a broad elliptical cross-section and shows distantly spaced constrictions. *B. haresi* Reeside (1927, p. 10, pl. 6, figs. 5–10; pl. 7, figs. 9, 10) of the Western Interior and *B. inornatus* Meek (1861) of the Pacific Coast are relatively smooth shells but are larger and have more incised sutures.

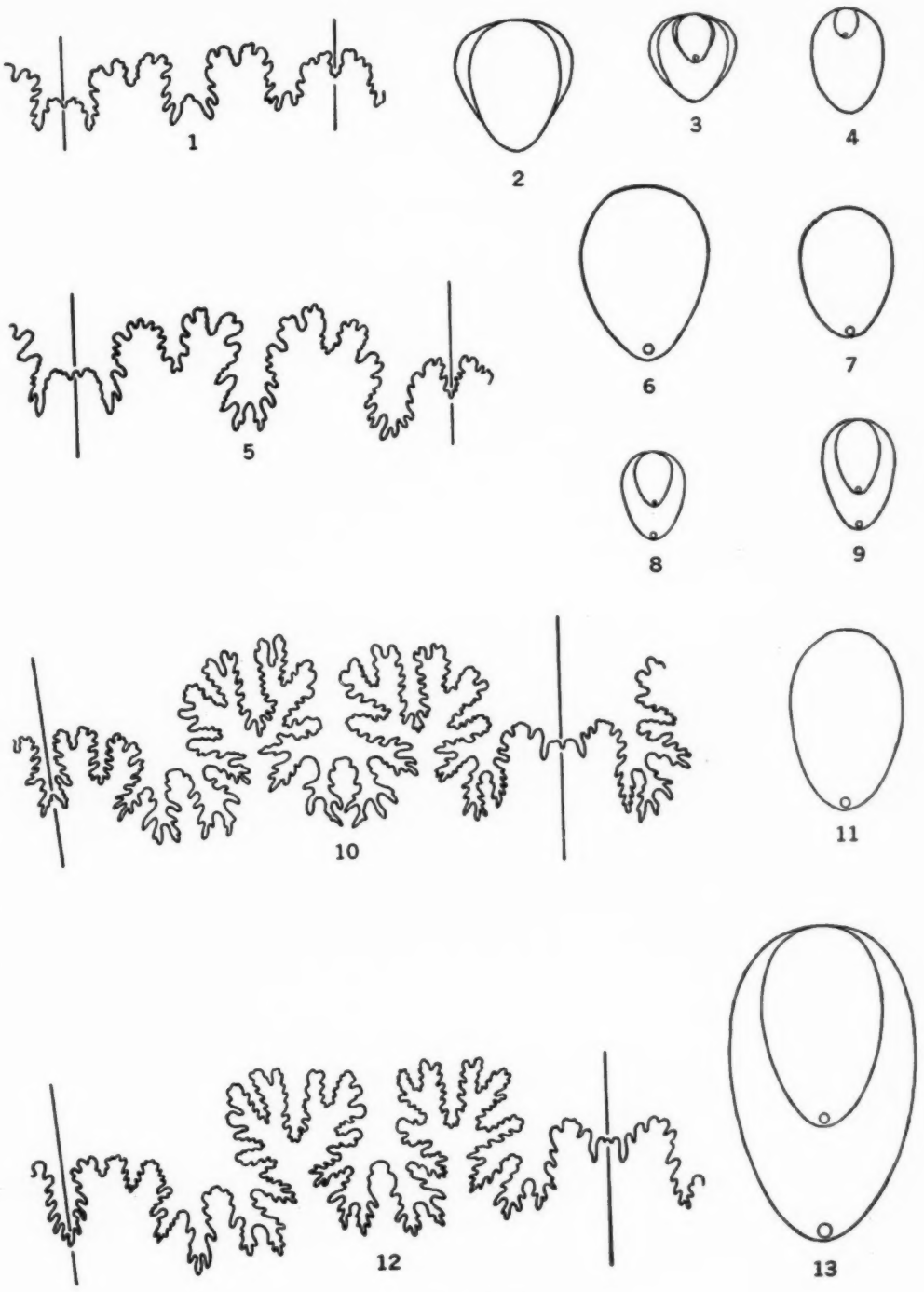
Smooth or nearly smooth baculites are known from many parts of the world. Of the European species, *B. vertebralis* Lamarck (=*B. faujasii* Lamarck), as figured by Van Binckhorst (1873), differs by its more elliptical cross-section, more rapid taper, and suture with broader and more incised lobes. The specimens of *B. vertebralis* figured by Picard (1929) from the Senonian of Palestine resemble *B. mariasensis* by their smooth shells and simple sutures but have nearly elliptical cross sections. *B. bailyi* Woods (1906) from South Africa is a small form with slight taper but has a suture with both narrow lobes and saddles. Several species from Madagascar are very close to *B. mariasensis*. The most common form, *B. besairiei* Collignon (1931, pp. 37, 38, pl. 5, figs. 6, 6a, 7, 7a, 8, 8a, 9; pl. 9, fig. 16), appears to differ mainly by its broader venter. *B. roedereri* Collignon (1931, p. 38, pl. 5, figs. 10, 10a; pl. 9, fig. 17) and *B. latelobatus* Collignon (1931, p. 38, pl. 5, figs. 11, 11a, 12, 12a; pl. 9, fig. 18) likewise have broader venters, but otherwise are very similar to *B. mariasensis*. The sutures of the Madagascar species differ from the American form by the second lateral saddle being considerably smaller than the first. *B. yokoyamai* Tokunaga & Shimizu (1926) of the lower Senonian of Japan also closely resembles *B. mariasen-*

FIGS. *1–13*

1–3—*Baculites sweetgrassensis* Cobban, n. sp. *1, 2*, Second from last suture, ×3, and cross-section, ×2, at large end of holotype; *3*, cross-sections of paratype, ×2. (p. 820)

4–7—*Baculites mariasensis* Cobban, n. sp. *4, 7*, Cross-sections, ×2, of paratypes (pl. 118, figs. *10, 11*); *5, 6*, eleventh from last suture, ×3, and cross-section, ×2, of small end of holotype. (p. 818)

8–13—*Baculites gregoryensis* Cobban, n. sp. *8, 9*, Cross-sections, ×1, of paratypes (pl. 118, figs. *4, 5*); *10, 11*, suture ×2, and cross-section, ×1, of small end of paratype (pl. 118, fig. *2*); *12, 13*, suture, ×2, and cross-sections, ×1, of holotype. (p. 820)



FIGS. 1–13

sis but differs by its elliptical cross-section and suture with the second lateral saddle much smaller than the first.

Occurrence.—*B. mariasensis* is abundant in the Colorado shale 380 to 635 feet below the top, on the Sweetgrass arch of north-central Montana. It is common in the upper part of the Frontier formation of the Wind River Basin of west-central Wyoming. The sandstones of the upper part of the Frontier formation are replaced northeastward by shale, and, along the flanks of the Big Horn Mountains, *B. mariasensis* occurs in the Cody shale several hundred feet above the top of the Frontier formation.

The types are from calcareous concretions in the Colorado shale, 514 to 525 feet below the top, at U. S. G. S. Mesozoic locality 21422, in the north bank of the Marias River, 5.5 miles south of Shelby, in NE¼ sec. 20, T. 31 N., R. 2 W., Toole County, Montana.

Types.—Holotype, USNM 106985; paratypes, USNM 106986, 106986a.

BACULITES SWEETGRASSENSIS Cobban, n. sp.
Plate 118, figures 6–9; text-figures 1–3

Shell small, scarcely tapering; cross-section broadly ovate. Sculpture consists of prominent, broad, node-like swellings that are arched with the concavity on the orad side. Each node is extended forward obliquely on its ventral side where it passes into a rib that crosses the venter with strong forward arching. The nodes are distantly spaced, the distance between nodes being about equal to 1.5 or 2 diameters of the intervening shell. The holotype, an internal mold largely made up of a nearly complete living chamber, attains a diameter of 9.5 mm.

The suture is simple and comparable to that of *Baculites mariasensis*, n. sp.

Remarks.—The small size, slight taper, distantly spaced arcuate nodes that pass into ventral ribs, and simple suture readily separate this form from other species with arcuate nodes. The nearest American species is *Baculites thomi* Reeside (1927, p. 13, pl. 12, figs. 9–14) from the Telegraph Creek formation which has opposite nodes connected by a strongly arched siphonal rib, but that is a larger species with more closely spaced nodes and more complex suture. *B. taylorensis* Alkins (1929) and *B. undatus* Stephenson (1941) have strong arcuate nodes but these are much larger species. The upper Turonian specimen figured by Kossmat (1897) as *Baculites*, n. sp., aff. *bohemicus* Fritsch, later referred to *B. kossmati* Nowak (1908, pp. 348, 349), shows some resemblance to *B. sweetgrassensis* by its small size, gentle taper, stout cross-section, and distantly spaced arcuate ribs that cross the venter. The latter, however, do not rise into prominent node-like swellings, and the suture is more incised. *B. boulei* Collignon (1931, pp. 35, 36, pl. 5, figs. 2, 2a; pl. 9, fig. 14) of the Upper Cretaceous of Madagascar is a scarcely tapering shell that shows resemblance to *B. sweetgrassensis* in its sculpture and suture, but it is a larger species with weaker and more closely spaced nodes.

Occurrence.—*B. sweetgrassensis* is an uncommon species that is known only from Montana in shale of lower Niobrara age. The types were collected with *B. mariasensis* in the Colorado shale, 514 to 525 feet below the top, on the Sweetgrass arch at U. S. G. S. Mesozoic locality 21422, in NE¼ sec. 20, T. 31 N., R. 2 W., Toole County, Montana.

Types.—Holotype, USNM 106983; paratype, USNM 106984.

BACULITES GREGORYENSIS Cobban, n. sp.
Plate 118, figures 1–5; text-figures 8–13

Shell fairly large, with rapid taper and compressed-ovate cross section. Dorsum and flanks smooth; venter smooth on small specimens and corrugated on larger ones. The holotype, a septate internal mold, attains a diameter of 45.5 mm.

The suture is complex. Its most characteristic feature is the first lateral lobe, which is constricted just above the major lateral branches.

Remarks.—This species is most closely related to *Baculites compressus* Say as figured by Meek (1876). *B. gregoryensis* differs by its smaller size, broader cross-section, smoother flanks, and by the details of the suture. The first lateral lobe of *B. compressus* is constricted between the terminal branches and the main lateral branches, whereas in *B. gregoryensis* the constriction occurs above the main lateral branches. The suture of

B. compressus var. *ornatus* Robinson (1945) of the basal part of the Bearpaw shale of Saskatchewan is intermediate between that of *B. gregoryensis* and typical *B. compressus*. The much younger *B. clinolobatus* Elias (1933) from Elias' Beecher Island member of the Pierre shale is a smooth form with a suture resembling that of *B. gregoryensis* but differs by its gentle taper and elliptical cross-section. One of the sutures figured by Nowak (1908, p. 331, fig. 10) and assigned by him to *B. anceps* Lamarck var. *leopoliensis* Nowak from the Upper Cretaceous of Poland cannot be separated from the suture of *B. gregoryensis*, but Nowak's variety is ribbed and the other sutures figured by Nowak (1908, p. 331, figs. 5–9) are much less incised. Of other European species, *B. knorrianus* Desmarest as figured by Schlüter (1876) is similar in being a relatively large, smooth shell with compressed cross-section, but the suture, although complex, does not show the first lateral lobe to be most constricted above the posterolateral branches. *B. hochstetteri* Liebus (1902) of the Carpathian Cretaceous is a smooth shell with rapid taper. The suture is complex with the lobes constricted at their bases.

Occurrence.—Baculites gregoryensis is known only from the northern Great Plains in marine rocks equivalent to the Judith River formation of central Montana. On the north flank of the Black Hills it occurs in a 200-foot gray sandy shale that immediately overlies the Mitten black shale member of the Pierre shale. Along the Missouri Valley in south-central South Dakota this species is present in the calcareous Gregory member of the Pierre shale. In both areas it is associated with *Pachydiscus complexus* (Meek), *Solenoceras meekanum* (Whitfield), and identical species of *Inoceramus*. The types are from the Gregory member at U. S. G. S. Mesozoic locality 21594, two miles west of Oacoma, in SE¼ sec. 22, T. 104 N., R. 72 W., Lyman County, South Dakota.

Types.—Holotype, USNM 106987; paratypes, USNM 106988, 106988a-c.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 6, P. 822, NOVEMBER 1951

NOMENCLATURAL NOTES

PLOTOSAURUS, A NEW GENERIC NAME FOR *KOLPOSAURUS* CAMP, PREOCCUPIED

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Dr. A. S. Romer has kindly informed me that *Kolposaurus* Camp 1942 (Memoirs Univ. Calif., vol. 13, p. 2) is preoccupied. According to Neave 1939 (Nomenclator Zoologicus) this name was given by T. G. Skuphos in 1893 (Abh. Geol. Reichsanstalt, Wein, vol. 15, Heft 5, p. 14) to a nothosaur, represented by vertebrae with bifurcate transverse processes. I therefore propose *Plotosaurus* (swimmer-lizard) as a substitute, with *Plotosaurus bennisoni* the genotype. *Plotosaurus* is a mosasaur from the Upper Cretaceous of California.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Mr. Francis Hemming, secretary of the Commission, has announced that application for suspension of the Rules has been made in connection with the following paleontologic names. Details are published in Vol. 2, part 11, and Vol. 6, parts 1 to 4, of the Bulletin of Zoological Nomenclature dated September 28, 1951.

Vol. 2, Part 11

Xiphosura Brünnich, 1771 (Merostomata), proposed suppression of, and validation of *Limulus* Müller, 1785 (pp. 319–323), File 506.

Vol. 6, Part 1

Trivial names *duplicatus* and *floriformis* Martin, 1809, published in combination with "*Erismatolithus Madreporites*" (Anthozoa) (pp. 7–17), File 461.

Trivial names *resupinatus*, *semireticulatus*, *productus*, *crumena*, *pugnus*, *trigonalis*, *subconicus*, and *striatus* Martin, 1809, published in combination with "*Conchyliolithus Anomites*" (Brachiopoda) (pp. 7–17), File 461.

Martinia McCoy, 1844 (Brachiopoda) (pp. 30–32), File 535.

Vol. 6, Part 3

Modiolus Lamarck, 1799 (Pelecypoda) (pp. 67–71), File 213.

Trigonia Bruguière, 1789 (Pelecypoda) (pp. 79–83), File 499.

Vol. 6, Part 4

Trivial name *quinqueloba* Goldfuss, 1831, published in combination with *Asterias* (Asteroidea) (p. 106), File 514.

Hoplites Neumayr, 1875 (Ammonoidea) (pp. 110–113), File 533.

Any person having knowledge of, or interest in, these names is invited to submit pertinent comments in writing to the Secretary, 28 Park Village East, Regent's Park, London, N.W.1, England. Comments should be identified by the file numbers noted above and, in order to be considered by the Commission, must be received by the Secretary before March 29, 1952.

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ANNUAL MEETING S.E.P.M.

Biltmore Hotel, Los Angeles

March 24-27, 1952

The annual meeting of the S.E.P.M. will be held at the Biltmore Hotel, Los Angeles California, on March 24, 25, 26, and 27, 1952. As in previous years the meeting will be held jointly with the A.A.P.G. and S.E.G.

In addition to presidential addresses and joint sessions with the other two societies, there will be separate technical sessions, symposia, and a field trip. The annual S.E.P.M. symposium will be on "Objectives in Modern Sedimentology and Paleontology." There will probably be another one on "Recent Marine Sedimentation." The field trip will be to type localities of several well-known formations which have excellent micro-faunas.

President Tom Philpott has appointed K. O. Emery, Geology Department, University of Southern California, Los Angeles 7, California to be program chairman for the S.E.P.M. Members planning to submit papers should notify the program chairman by Dec. 15 of the title and length of their papers. Abstracts, typewritten, double-spaced, and in duplicate, are due on or before Jan. 1.

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